SILURIAN MYODOCOPID OSTRACODES: THEIR DEPOSITIONAL ENVIRONMENTS AND THE ORIGIN OF THEIR SHELL MICROSTRUCTURES

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ABSTRACT. European Silurian myodocopid ostracodes form part of an almost exclusively pelagic, recurring faunal association. In general, they are facies related to typically laminated mud-silt or carbonate sequences deposited in relatively quiet, low energy, probably outer shelf to shelf slope environments. Their palaeogeographical and facies distributions may in part be due to depth control.

Reticulation, corrugation, and tuberculation are recognized as the true, genetically controlled external shell ornament in Silurian bolbozoid and 'cypridinid' myodocopids. In contrast, enigmatic polygonal and associated radiate shell microstructures, described from a wide variety of Silurian myodocopids, are interpreted as the surface expression of calcium carbonate platelets and possibly the result of *in vivo* shell calcification and post-mortem 'diagenetic' changes; they cannot, therefore, similarly be used in taxonomy.

A model based on analogues in Recent myodocopids and on possible variation in the pattern of nucleation centres in the shell is proposed to explain the mode, variety of styles, intraspecific, and ontogenetic variation of shell calcification in typical Silurian myodocopids. Pore canals may be the nucleation centres of calcium carbonate. If centres are numerous and densely arranged, this may account for the formation of closely packed, polygonal microstructural patterns on (and through) the shell. If nucleation centres are sparser and distant, calcification possibly terminates before all platelets can coalesce, thus accounting for observed patterns of isolated to clustered platelets of various larger sizes. Radiate ('rosette') type platelets are possibly produced when post-mortem acicular recrystallization affects various sized platelets. Smooth valves may represent newly moulted individuals; patches of platelets might indicate poor or an intermediate stage of calcification; specimens with densely packed platelets may have completed cuticle calcification.

THE last thirty years have witnessed substantial research on several major faunas of Silurian ostracodes (e.g. see Siveter 1978, 1980) but no monographic study has encompassed Silurian representatives of the extant order Myodocopida. Though treated in part by Canavari (1900) and Bouček (1936), our primary taxonomic knowledge of the group in the Silurian still relies largely on the work of Barrande (1872) and Jones (1861, 1873, 1884). However, as Siveter (1984) has shown, Silurian myodocopids are important and unique ecologically in possibly representing pioneer pelagic ostracode stock and they have unfulfilled biostratigraphical and biogeographical potential. This paper is our first of an intended series on British, Czechoslovakian, French, and Sardinian Silurian myodocopids (see also Palmer and Gnoli 1985) which will test this potential. We address a problem fundamental to classification within the group: what is the nature of their true external ornament and what is the nature, origin (biological or 'diagenetic'?), and significance of enigmatic microstructures which we have recognized in the shell of many types of Silurian myodocopids? Essentially, which of these characters can, and which cannot, be used taxonomically? In addition, we outline the distribution, depositional setting, and palaeoecology of Silurian myodocopids.

Herein myodocopid refers to Silurian myodocopines of two broad taxonomic groups, bolbozoids and 'cypridinids' (text-fig. 2). Entomozoid ostracodes (Silurian–Carboniferous) have traditionally been placed alongside the bolbozoids (in the Entomozoacea; Sylvester-Bradley *in* Moore 1961), with which they often occur in space and time in the Silurian. However, we would support a notion that the 'entomozoid' group (as currently, but erroneously, understood and used in the literature, e.g. forms such as *Entomis migrans*) is not closely related to typical myodocopines.

Silurian myodocopids are restricted mainly to finely laminated, fine-grained clastic sediments,

where they often occur in substantial numbers, with a recurring association of graptolites, nautiloids, and bivalves. They are typically preserved as mould faunas and partly for that reason have been so neglected.

By examination of our abundant, newly collected Silurian myodocopid material from Wales, France, and Czechoslovakia, and comparison with Recent myodocopids, it is concluded that the microstructures described herein from the Silurian shells are probably manifestations of both the calcification process and, to varying degrees, a diagenetic overprint. Such microstructures cannot, therefore, be used as characters in taxonomy. In order to explain the variety of observed shell microstructures in Silurian myodocopids, a model outlining possible modes of shell calcification in such groups is proposed.

EUROPEAN DISTRIBUTION OF SILURIAN MYODOCOPIDS

Both their morphology and pattern of distribution suggest a pelagic mode of life for typical Silurian myodocopids (Siveter 1984). European Silurian myodocopids are currently known from the Wenlock–Pridoli time interval and occur in the Welsh Basin of Britain, the Armorican Massif and Montagne-Noire of France, the Barrandian basin of Czechoslovakia, Poland, Sardinia, Portugal, and Spain (text-fig. 1). Although the range of facies within which they occur in these areas is somewhat restricted, this is an otherwise widespread geographic distribution, and contrasts with a generally more restricted distribution known from other Silurian ostracode assemblages. For example, Silurian ostracode faunas from Czechoslovakia (Bouček 1936) are dominated by non-palaeocopes and are substantially different in overall composition from contemporaneous, beyrichiacean rich faunas of northern Europe (e.g. Britain, Baltoscandia) and eastern North America (Siveter MS). In this case, though the barrier of the incipient 'mid-European' Rheic Ocean was perhaps hindering the dispersal of some invertebrate groups such as benthic palaeocopes and non-palaeocope ostracodes, the same was certainly not true of myodocopid ostracode species. Moreover, some Silurian myodocopids also occur in North Africa (unpublished information) and, for example, Australia (Jones 1861, 1873, 1884; De Koninck 1876; Strusz, pers. comm.). Because of this 'great extension of this old creature's habitat . . .' Jones (1884, p. 393) suggested a 'truely pelagic nature' for some '*Entomis*' myodocopids.

Localities and material. The material studied amounts to several thousand specimens from the following areas and localities. Information on the localities of all our collections will be given in later papers.

Armorican Massif, France. Localities in Ille-et-Vilaine, Mayenne, Sarthe, and Finistère. Their ages are determined typically using graptolites or chitinozoans, but are generally imprecisely known. Current studies on new graptolite collections may provide more finely resolved age determinations.

1. 'Les Buhardières'; exposure along D104 road between Saint-Germain-le-Fouilloux and Andouillé, Mayenne; Laval Synclinorium.

2. 'La Cultais'; outcrops near 'La Cultais' farm, Vieux-Vy-sur-Couesnon, Ille-et-Vilaine; Menez-Bélair Synclinorium. See Paris 1977, 1981.

Localities 1 and 2 belong to the upper part of La Lande Murée Formation (Paris 1981 and pers. comm.). The sediments ('ampelites') are grey to black, finely laminated shales. Trace and major element geochemical studies show that, as with most Silurian black shales, these sediments are highly organic- and Vanadium-rich (Dabard 1983; Dabard and Paris 1986). The ostracodes occur as abundant, slightly tectonically deformed internal and external moulds. Associated fossils include graptolites, small, thin-shelled bivalves, fragments of orthoconic nautiloids and disarticulated eurypterid, and phyllocarid crustacean ('*Ceratiocaris*') remains.

The cleavage prevents accurate determination of the graptolites at locality 1 but there are clearly numerous pristiograptids of the *P. dubius* type, some *Monoclimacis* cf. *haupti*, and long distal fragments of slender monograptids with simple, straight thecae and unelaborated thecal apertures of the *nilssoni/progenitor* type. Until the proximal ends are found, confident identification cannot be made and the possible stratigraphic range of this locality extends through a large part of the Ludlow (D. Palmer). Graptolites of locality 2 indicate an upper Ludlow to lower Pridoli age (Jaeger, *in* Paris 1981).

3. 'Le Moulin de Régereau'; exposure along the road between Origné and l'Huisserie, Mayenne; Laval Synclinorium. See Peneau 1936; Paris 1981. The sediments consist of siltstones and mudstones of assumed
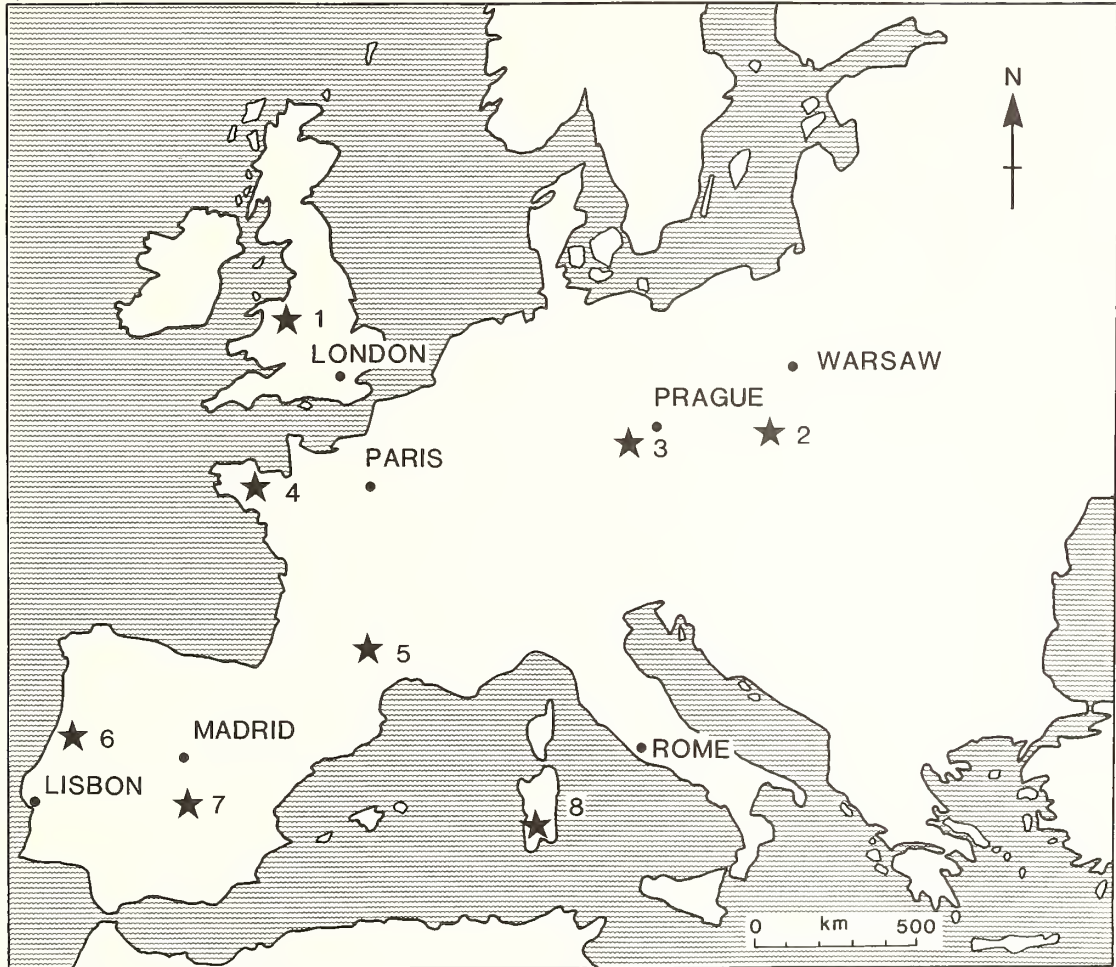
TEXT-FIG. 1. Distribution of the main faunas of Silurian myodocopid ostracodes in Europe. 1, Welsh Basin (Siveter 1984; Siveter and Palmer, in prep.). 2, Poland (Gürich 1896). 3, Bohemia (Barrande 1872; Bouček 1936; Siveter and Palmer, in prep.). 4, Armorican Massif (Siveter, Vannier and Palmer, in prep.). 5, Montagne-Noire (Chaubet 1937). 6, Portugal (unpublished information). 7, Spain (unpublished information). 8, Sardinia (Canavari 1900).

Pridoli age (Paris 1981). Rare ostracodes are associated with bivalves, the crinoid '*Scyphocrinites*', and fragments of '*Ceratiocaris*', all decalcified and preserved as moulds.

4. Chemiré-en-Charnie, Sarthe; Laval Synclorium. Siliceous nodules collected by Guillier (Guillier and de Tromelin 1874; Guillier 1886) and deposited at the Musée d'Histoire Naturelle de Nantes, Loire-Atlantique.

5. Saint-Denis-d'Orques; outcrop at the intersection of the Laval to Le Mans motorway and the Saint-Denis-d'Orques to Brûlon road, Sarthe; Laval Synclinorium.

Localities 4 and 5 consist of siltstones and mudstones containing numerous, partly pyritized nodules in which the ostracodes (myodocopids and palaeocopes) occur as normally well preserved and undeformed moulds of single valves or closed carapaces. The diverse fauna includes crinoids, fragments of the phyllocarids *Ceratiocaris* and *Schugurocaris* (I. Rolfe, pers. comm.), the rhombiferan echinoderm *Lophotocystis* (J. Chauvel, pers. comm.), and graptolites of Ludlow or Pridoli age (D. Palmer).

Welsh Basin. We have collected Silurian myodocopids from many localities in this region, mainly in the Long Mountain district but also from the 'Radnor' and 'Denbigh' areas. Material studied specifically for the present paper comes from just two localities (1, 2).

1. Cause Castle Farm (SJ 341 077), Long Mountain, Shropshire.

This is one of about 100 localities in the Long Mountain yielding infrequent myodocopid ostracodes, which generally occur scattered throughout the laminated muddy siltstone facies of the Ludlow Long Mountain Siltstone Formation and succeeding Causemountain Formation (Palmer 1970). At this locality (= LMS Formation) some silt laminae are crowded with the moulds of finely comminuted shell debris, plus a few small but entire shells (e.g. lingulids), crinoid columnals, and eurypterid and phyllocarid fragments. Associated are occasional large myodocopid valves and numerous graptolites, *Saetograptus leintwardinensis*, the index for the eponymous, basal Ludfordian zone.

2. Friends Meeting House Quarry (SO 138 641), Llandegley, Powys.

Apart from the Long Mountain, the 'Radnorshire' area (now in Powys) is the only part of the Welsh Basin to have yielded a large number of myodocopid bearing localities, some twenty-two being cited by Kirk in her unpublished thesis (1947). Most occur in her 'Striped Flag Series', which consists of finely laminated and banded or 'striped' admixtures of mud and silt, generally with planar lamination or small scale cross-stratification. The characteristic, autochthonous fauna of the Striped Flags consists of graptolites, orthocones, and bivalves. Minor associates include myodocopids, rare crinoids, phyllocarids, and small brachiopods such as *Aegeria grayi* and *Lingula lata*. Intercalated south to south-east derived slump sheets often introduce an allochthonous, shelf shelly fauna into the area. The Striped Flags encompass the Ludlow *N. nilssoni*, *L. progenitor* (see Palmer 1970), *L. scanicus* s.l., and *P. tumescens/S. chimaera* graptolite zones. However, Kirk also records rare myodocopids in strata as old as the '*vulgaris*' (= *ludensis*) Zone and as young as the *S. leintwardinensis* Zone, and immediately above. Thus the total range for myodocopids in 'Radnorshire' is essentially the same as in the Long Mountain. Friends Meeting House Quarry comprises typical 'Striped Flags' lithology and mould fauna, and lower Ludlow, *C. scanicus* Zone, graptolites including *C. scanicus* s.l., *S. varians*, *S. chimaera semispinosus*, *P. dubius*, *P. tumescens*, and *B. bohemicus* (D. Palmer).

The geological survey of the 'Denbigh' area, Clwyd, resulted in finds of a few scattered Silurian myodocopid localities in North Wales (Warren *et al.* 1984). Here, myodocopids appear to be relatively very rare, but their stratigraphic distribution is broadly as in the Long Mountain, specimens being scarce in the upper Wenlock (*C. lundgreni* Zone), somewhat commoner in the Ludlow (*N. nilssoni* to *C. scanicus* zones) and again less common higher in the Ludlow (up to and including the *S. leintwardinensis incipiens* Zone; younger Silurian strata are not preserved). Both their facies and faunal associations are the same as elsewhere in the Welsh Basin. The myodocopids occur mainly in the 'ribbon banded mudstone' (Warren *et al.* 1984, pp. 44–46) of the Nantglyn Flags Group (straddling the Wenlock–Ludlow boundary) and the higher Elwy Group (Ludlow), a facies virtually identical to the 'Striped Flags' of the Radnor area. Its faunas are dominated by graptolites accompanied by orthoconic nautiloids and bivalves (particularly cardiolids) and also include crinoids (especially scypho-crinitids; Warren *et al.* 1984, p. 44) which are sometimes preserved complete and occasionally with orthocone 'substrates'.

Czechoslovakia. Silurian myodocopids in Czechoslovakia are predominantly of Ludlow age. Some of Barrande's original localities were either small and isolated from the main outcrop, and are now unidentifiable, or were poorly localized within thick sections so that they are now also unavailable. However, modern investigations by Czech palaeontologists have resulted in new exposures at the same horizons, yielding faunas similar to those of the 'lost' localities. For example, Barrande's type locality for '*Bolbozoe*' *bohemica* can no longer be located at Vyskočilka, but this species can still be obtained (DJS) from a similar horizon (*C. scanicus* Zone) on Holý Vrch Hill at Lounín near Zdice. Here, as in other Czechoslovakian Ludlow localities, the myodocopids are often abundant as moulds or as degraded carbonate shells in thin, platy, planar laminated, muddy limestones and are accompanied by orthoconic nautiloids, graptolites, and occasional bivalves.

Preservation. The vast majority of myodocopids we have studied are preserved as moulds. This may be as much the result of their occurrence in particular sedimentary environments or lithologies (fine-grained clastics), where virtually all the calcareous-shelled fossils have been dissolved, and/or as a product of the thinness of their shells. Exceptions are found where myodocopids occur in limestones (e.g. Sardinia) and then, although recrystallized, shells can be preserved as carbonate; however, we have not yet studied in detail this important mode of preservation.

Sedimentary matrix. That the types of deposit in which European Silurian myodocopids have so far been found are rather restricted could in part be preservational due to their relative fragility. The curiously impersistent stratigraphic record of the group since Silurian times supports this contention. Nevertheless, the limited facies pattern of occurrence of our Silurian species requires further explanation, especially since the group in general is considered to be pelagic.

The sediments in which our Silurian myodocopids are found are characteristically laminated and lack any indication of bioturbation or hardly any of the contemporaneous representatives of the typical brachiopod-dominated, shelly (shelf) faunas. Sedimentologically, they occur in a three component system of muds, muddy silts, and carbonate. A main feature is the fine (silt or smaller) grain size of the terrigenous material compared with the larger size of much of the carbonate 'clast' material, which is essentially made up of whole fossils and thus derived from within the depositional environment. Most of the myodocopid-bearing deposits consist of closely spaced planar laminations which result from either alternations of 'clean' silt laminae with muddy silts or, muddy silts with dark hemipelagic muds. Less commonly the latter may predominate, as in the dark grey (originally black?; but now chloritized) shales of Brittany. Because of the fine grain size, the moulds of the Brittany myodocopids preserve exquisite details of shell structure. Increase in the bioclastic component of the sediment in the Bohemian and Sardinian myodocopid-bearing strata tends to diminish but not destroy lamination, as the fossils themselves are commonly arranged as parallel orientated, bedding plane assemblages. This results in a coarse 'grain' parting lineation (see Gnoli *et al.* 1979, figs. 2 and 9a).

The bioclastic component varies greatly in volume and grain size, sometimes forming only a small proportion of the sediment (1 % volume in some Welsh Borderland localities), especially where muddy silts predominate and there are only very rare macrofossils which are almost invariably preserved as moulds. In the middle of the range are the highly fossiliferous, but now decalcified, hemipelagic muds of Brittany and the similarly fossiliferous, fine grained, laminated, and shaley micrites (microsparites) typical of the Bohemian localities. In contrast, myodocopid-bearing coquinoid 'cephalopod' limestones of Sardinia have a small terrigenous clastic component (5 %; Garuti *in* Gnoli *et al.* 1979) and consist largely of complete shells of all sizes in a micrite matrix.

Certain sedimentary characteristics appear common to almost all the myodocopid-bearing deposits of this study, thus suggesting similar underlying parameters in their mode of deposition. In particular, the fineness of the non-organic clastics and the prevalence of close spaced, planar laminae seem to indicate a relatively 'quiet' but not static depositional environment (except perhaps as represented by the black shales of Brittany) debarred from both the massive turbiditic input of terrigenous material often associated with deep basins and from the rigours of high energy and coarse (tidal) clastics of shallow shelves. Most of the inorganic sediment (muddy silt) was seemingly deposited as turbid flows of low velocity and of no erosive power, which were frequently and intermittently introduced into areas experiencing a low level 'rain' of hemipelagic mud. Gentle bottom traction currents reworked the surface layers of the 'homogenised', structureless muddy silt layers to form winnowed, often micaceous, 'clean' silt laminae. The overall result was to produce the 'Striped Flag' or 'ribbon banded mudstone' type of lithology, with its alternations of muds, muddy silts, and silts. Currents were of the appropriate strength to orientate fossils (e.g. orthocones and graptolites in the Welsh Basin localities) without any size sorting (e.g. of bivalved organisms) or much abrasion or fracture (ostracodes and bivalves may be articulated), and sometimes to produce a parting lineation or small scale, wispy cross-lamination but no other depositional or erosional structures. In Bohemia, for example, it is common for the orthocones and graptolites to show parallel orientation consistently throughout several centimetres of strata, indicating bottom currents of fairly persistent velocity and direction over a considerable timespan (Petránek and Komárková 1953; Turek 1983).

Although the volume of terrigenous silt and mud is relatively low in Bohemia and virtually absent in Sardinia, there is similar evidence of both having been depositional areas again debarred from both deeper water turbiditic and shallow shelf clastic depositional processes. The carbonate that is present shows no reefal or other shallow water structures. Indeed, the dominant bioclastic components can

be diagnosed quite differently (see below) and their presence is possibly the result of both a primary lack of sediment to 'dilute' the accumulating shelly remains and secondary accumulation by currents.

Numerical occurrence and faunal associates of myodocopids. The frequency of occurrence of European Silurian myodocopids is generally very low and is partly why they have received so little attention. Moreover, they tend to occur in comparatively low diversity faunas, which lack the more commonly studied members of the Silurian shelf benthos. Some idea of their frequency can be gained from studies in the Long Mountain, a sequence more thoroughly investigated (by D. P.) in terms of its myodocopid and associated fauna than any other Silurian myodocopid-bearing area. Their distribution throughout the laminated siltstones of some 1500 fossiliferous localities of Ludlow age is diffuse, only about 7% yielding myodocopids, which generally comprise less than 10% of the fauna of each locality. That a previous investigator of the Long Mountain sequence (Das Gupta 1932) did not record any myodocopids, also reflects their relative scarcity.

Whilst the basis for comparing the various localities and areas (text-fig. 1) arises from the presence of myodocopids, we also recognize a number of features in common in the associated faunas, although the taxa may differ even at the family level and different members may dominate in particular localities. We are essentially dealing with a known but little studied and relatively low diversity graptolite–orthocone–bivalve faunal association, whose minor members include various arthropods (ostracodes, phyllocarids, eurypterids, and rare, small trilobites) echinoderms (mainly crinoids, small pisocrinids, and scyphocrinitids), and a few brachiopod species (small lingulids and chonetids).

In Welsh Borderland myodocopid-bearing localities, graptolites and occasional small bivalves tend to dominate the faunas, with orthocones or myodocopids next most abundant. All other associated organisms tend to be very rare. The fauna from Cause Castle Farm, Long Mountain, is graptolite dominated, with the associated myodocopids, lingulids, phyllocarids, and crinoid columnals being current assembled on clean silt laminae. Generally in this area of the Long Mountain, graptolites and occasional small pterineid bivalves (up to 400 individuals/m^2) predominate. Myodocopids are slightly more abundant at Friends Meeting House Quarry, where even so, they comprise only about 10% of a generally sparse, graptolite dominated fauna and are, once more, scattered at very low densities throughout 3–4 m of laminated muddy silts. Here, fossils tend to be more abundant in the hemipelagic muds, especially on certain bedding planes. They are also present, but much less common, scattered throughout the muddy silts, their concentration being 'diluted' by the frequent incursions of sediment. Higher frequencies may again be encountered on the winnowed silt laminae, where they may have been concentrated by the removal of the mud or by current transport.

Compared with these Welsh occurrences, myodocopids can be much more abundant in the few localities in Bohemia and Brittany that have yielded them since the pioneer work of Barrande (1872), Barrois (1886), and Kerforne (1901). In the platy limestones of Bohemia graptolites and orthocones are common but faunas tend to be predominantly myodocopids, with some bedding plane assemblages achieving densities of 400 myodocopid individuals/m^2. Even greater abundances occur in the black shales of Brittany, where densities of 2000/m^2 or more are common and where, at some of the cited localities, ostracodes may dominate in comprising over 90% of individual assemblages. However, myodocopine s.s. valves are not always dominant, since the same bedding planes in Brittany may also have greater numbers of a smaller, thin shelled (and consequently poorly preserved) entomozoid ostracode. In the coquinoid (cephalopod) limestones of Sardinia orthoconic nautiloids tend to be the dominant group. However, some limestone blocks contain graptolite dominated assemblages and/or abundant entomozoid myodocopids (see Palmer and Gnoli 1985 for geological background). The accompanying faunas are slightly more diverse than elsewhere, with taxonomically richer assemblages of bivalves and phyllocarids (Gnoli and Serpagli 1984). Again, the orthocones and graptolites show parallel orientation (Gnoli *et al.* 1979) and the vagaries of faunal composition may reflect fluctuations in bottom traction current strength.

Mode of life. European Silurian myodocopids are clearly part (albeit often a minor one) of a recurring faunal association generally dominated by organisms which are usually considered to be pelagic, either as virtually passive drifters (the planktonic graptolites and scyphocrinitids), or as active swimmers (the nektonic cephalopods, myodocopids, phyllocarids, eurypterids, and small spinose trilobites) at various levels within the water column. Only the bivalves and rare, small brachiopods appear to have been benthic, although doubts have been raised over such an interpretation for the mode of life of representatives of both groups (Watkins 1978, pp. 51–52; Kříž 1969, pp. 111–114; Nye *et al.* 1975). The main bivalve groups present are praecardiaceans *sensu* Newell (1969) and pterineids. The praecardiaceans are largely endobyssate suspension feeders and constitute the only possible (semi-) infaunal representatives. The pterineids are epibyssate suspension feeders (Kříž 1984).

The occasional presence of abundant small pterineids is significant since they may have been the only genuine, flourishing, autochthonous shelled benthos in areas where myodocopids are found. Their abundance in all growth sizes, often with both valves, indicates that their associated bottom conditions were unlikely to have been foul and toxic. Since they also occur in finely laminated muddy silts with no indication of bioturbation, the near surface sediments may have been deficient in oxygen, sufficient to prevent the establishment of an infauna. This possibility is supported by the presence of disseminated, fine-grained, framboidal pyrite within the muddy silts. The few other benthic fossils, found on clean silt laminae, are representatives of some of the most common epibenthic brachiopod species characteristic of the shelf. They are clearly allochthonous, transported individuals.

Epizoans are very rare, consisting mainly of spirorbids, bryozoans, and small crinoids attached to orthoconic nautiloids in the Welsh material, and spirorbids attached to phyllocarids in some of the French material. Since all surfaces of the orthocones tend to be colonized, it seems that colonization happened either *in vivo* or post-mortem, but whilst the shell of the host was still buoyant, rather than after it lay on the substrate.

Environments of deposition. All the evidence suggests that the relevant depositional areas were not within normal epicontinental shelf water zones, but were more likely to have been in either outer shelf to shelf margin or even shelf slope environments. Of the areas considered, the Welsh basin is perhaps best known and understood, with its 'Striped Flag' and 'ribbon banded mudstone' lithologies representing sedimentation against a background deposition of dark laminated hemipelagic mud. This 'tranquil' depositional environment was frequently interrupted by incursions of turbid mud-silt suspension flows, depositing occasionally graded but otherwise structureless thin muddy silt layers (1–5 cm thick). The substrate surface was also reworked by low velocity bottom currents, which winnowed out the fines and left thin, 'clean' silt laminae and shell lags, with the elongate fossils becoming parallel orientated. The thinness and high frequency of repetition of these sediment layers is sufficient for them to be compared with present-day marine, 'varve'-like (non-glacial) deposits. The sedimentation model (Thornton 1984, p. 388 *et seq.*) for the latter has hemipelagic muds settling out during the summers, the organic content being heightened by algal blooms. During winters, increased river run off leads to an increased supply of terrigenous material of which the fines (mud and silt) are carried out across the shelf in turbid suspension by storms. The resulting deposits are the thin, structureless or graded mud-silt layers.

In the Long Mountain area, the frequent colonization of the sea floor only by abundant small pterineid bivalves suggests that here Ludlow water depths were too great for the brachiopod dominated faunas of the shelf. The viability of the bivalve faunas also shows that bottom conditions were at times neither anoxic nor too turbid for suspension feeders to flourish. Yet (see above), oxygen depletion may have occurred within and virtually up to the sediment-water interface. In 'Radnor' and 'Denbigh' the intercalated slumps in the 'Striped Flags' suggest an intermittently unstable slope environment.

Compared with the Welsh area, Brittany includes what almost certainly was a stagnant anoxic basin with only hemipelagic mud deposition and a planktonektonic fauna. The ostracode rich Ludlow limestones of Bohemia are in many ways similar to the Welsh sediments but with a lesser proportion of terrigenously derived silt. This fraction is replaced by fine-grained bioclastic carbonate

derived from the organically rich carbonate shelf. Recent work on the implosion of cephalopod shells from this area (Westermann 1985) indicates outer shelf depths (> 300 m) for these deposits. Certainly there is again neither infauna nor shallow shelf epibenthos.

The Sardinian limestones differ in that they are almost wholly bioclastic carbonate (often entire shells, not size-sorted) with a minute proportion of hemipelagic mud and minimal terrigenous material. For the depths of deposition of the limestones Jaeger (1976) suggests deep water within Palaeotethys whilst Gnoli *et al.* (1979) prefer shallower shelf conditions but with anoxic bottom waters. Westermann's criteria have yet to be applied to the orthoconic nautiloids of this area.

Geographical distribution. The apparent contradiction posed by the supposed pelagic mode of life and the somewhat restricted geographical distribution of Silurian myodocopids exists not only in terms of their facies occurrence, but also in a wider palaeogeographical context. Contemporaneous shelf sediments in, for example, the Welsh Borderland of the Welsh Basin have probably been as closely examined as any sediments for their fossil content and yet while almost no myodocopids have been recorded other representatives of the faunal association are known. Furthermore, myodocopids are unknown from the Silurian rocks of Scandinavia, the USSR, or North America. Apart from France, England, Czechoslovakia, and Sardinia, myodocopids are also known (but unstudied) from Poland, Spain, and Portugal (text-fig. 1), Morocco, Australia, and possibly China. Clearly the overall distribution of Silurian myodocopids is enigmatic and needs explanation based on further studies. It is possible, at least in the case of their best-known (narrow) belt of occurrence encompassing western Britain, Brittany, Bohemia, and Sardinia, that myodocopids had some depth control or preferred vertical range (e.g. 200–500 m) that resulted in their remains being restricted to marginal shelf sediments. A variation on this would arise if they were nekto-benthic, as envisaged for longicone nautiloids with strong septa (Westermann 1985, p. 91) and again restricted to substrates at water depths of about 200–500 m.

MORPHOLOGY OF SILURIAN MYODOCOPID OSTRACODES

All of the Silurian myodocopids treated in detail and figured herein, from France and Britain, are based on mould material. Casts of external moulds were prepared with Silicone rubber using the technique described by Siveter (1982).

Pending current studies on their systematics, most of the Silurian myodocopids of this paper are cited under open nomenclature. However, in interpreting the microstructural and sculptural features of their shells it is necessary to outline features of their carapace morphology. The Silurian myodocopids discussed herein fall into two broad taxonomic groups, bolbozoids and 'cypridinids' (text-fig. 2).


EXPLANATION OF PLATE 83

Examples of true ornament in Silurian myodocopid ostracodes.

Figs. 1, 3, 5, 7, 8. Bolbozoid gen. et sp. nov. A. Right valve, IGR 33040, La Lande-Murée Formation, Les Buhardières (Andouillé, Mayenne), Armorican Massif, France. 1, lateral view, × 18. 3, detail of tubercles with pores, posteroventral part of valve, × 180. 5, single pores and (?) double pore-like structures in the anteroventral part of the valve, × 150. 7, detail of (?) double pore-like structure (from 5), × 505. 8, detail of single pore (from 5), × 505.

Figs. 2, 4, 6. '*Bolbozoe*' sp. nov. A. Left valve, IGR 33048, La Lande-Murée Formation, La Cultais (Vieux-Vy-sur-Couesnon, Ille-et-Vilaine), Armorican Massif, France. 2, lateral view, × 36. 4, detail of corrugated surface on either side of posterior sulcus, × 96. 6, detail of ventral part of the valve showing corrugations surmounted by four tubercles, × 165.
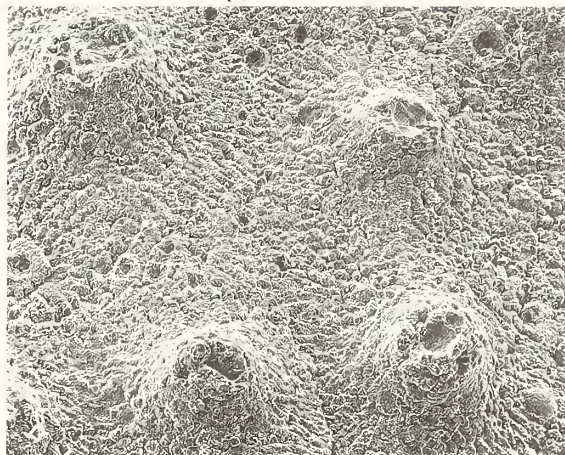
All specimens are silicone rubber casts from external moulds. All SEM except fig. 2. IGR = Institut de Géologie de l'Université de Rennes.
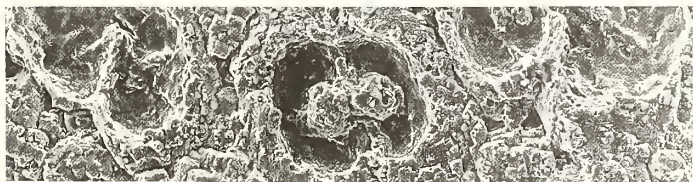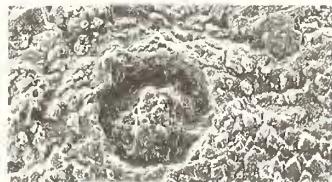
PLATE 83
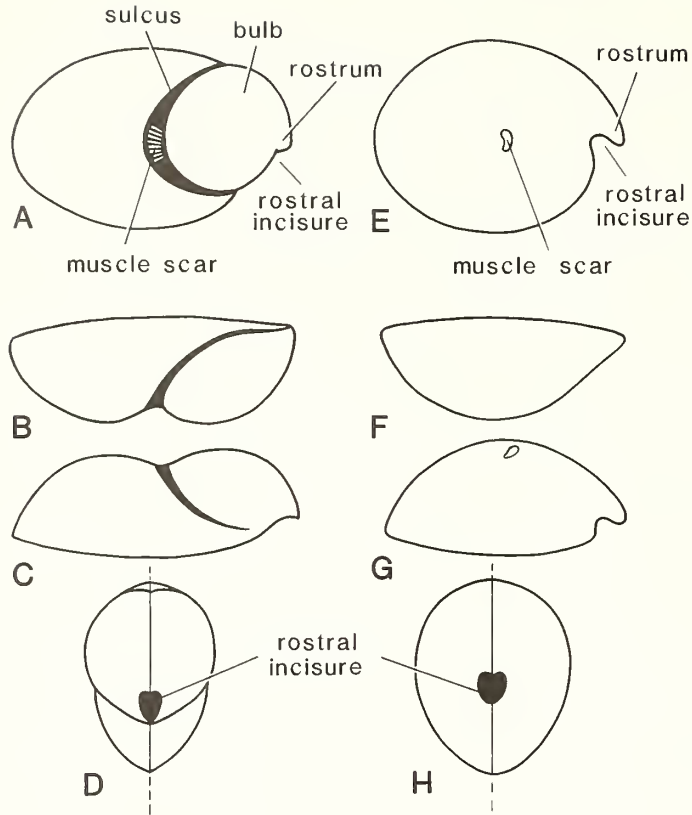

SIVETER, VANNIER and PALMER, Silurian myodocopid ostracodes
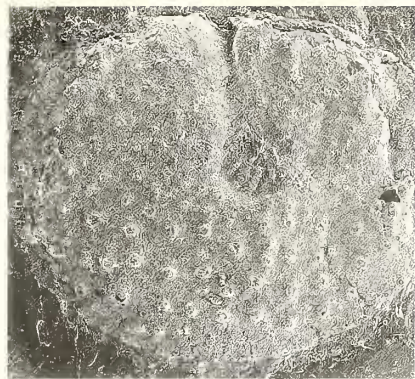
TEXT-FIG. 2. Morphological features of two groups of Silurian myodocopid ostracodes: A–D, a bolbozoid; E–H, a 'cypridinid'. A, E, right lateral views; B, F, dorsal views of right valves; C, G, ventral views of right valves; D, H, anterior views of carapaces.

Many of the Silurian myodocopids show plastic deformation of the valves and clear adductor muscle scar impressions externally on their valves, both of which suggest the occurrence of a rather thin, flexible but flimsy shell (Siveter 1984). Taken together with their geographical distribution and the fact that many have an anterior rostrum and rostral incisure (suggesting the presence of protruding, possible swimming appendages, e.g. see Kornicker 1975; fig. 141*a*, *b*), many Silurian myodocopids such as bolbozoids can be reasonably interpreted as pelagic ostracodes (Siveter 1984).

Bolbozoids (text-fig. 2A–D). These unusually large ostracodes are characterized by having a huge anterodorsal bulb delimited posteriorly and ventrally by a deep adductorial sulcus (e.g. Pl. 83, figs. 1 and 2; Pl. 84, figs. 2, 6, 7; Pl. 85, fig. 3; Pl. 86, figs. 1, 2, 5, 6), and are assigned to the Family Bolbozoidae (e.g. Siveter 1984). A sigmoidal, posterior sulcus (e.g. Pl. 84, figs. 2 and 7) and a caudal process (e.g. Pl. 83, fig. 2) occur in some forms. Undeformed, non-flattened material from the Armorican Massif and Bohemia confirms that the lobal surface of most bolbozoids is quite strongly convex. The function of the anterodorsal bulb, which is often larger and more hemispherical in instars, is speculative. Bearing in mind its position, that it often shows plastic deformation which possibly indicates a thin shell, and the fact that except for its ventral-most region it is consistently the only part of the lobal surface to lack ornament in several types of bolbozoids (see text-fig. 5), it is possible that the bulb on each valve was the site of some form of visual organ. Silurian bolbozoid and 'cypridinid' myodocopids clearly exhibit a prominent anterior rostrum and rostral incisure (identified in three-dimensional, closed carapaces; see text-fig. 2) like those of Recent myodocopids (cf. Pl. 84, figs. 1 and 2 with Pl. 88, figs. 1, 3, 5–8).

A radiate adductor muscle scar pattern, consisting of a series of narrow, closely spaced, alternating

ridges and grooves near the base of the vertical part of the adductorial sulcus, occurs in many Silurian bolbozoids. In some the pattern is simple, consisting of a few ridges and grooves of equal width, converging toward the bulb (e.g. Pl. 83, fig. 1). Others have a more complex, feather-like arrangement, composed of two unequal series of radiate ridges and grooves converging on a narrow, median (external) ridge curved parallel to the margins of the adductorial sulcus (e.g. Pl. 84, figs. 2 and 8; Pl. 87, fig. 6; text-fig. 3; and Gürich 1896, pl. 15, fig. 12, for *Bolbozoe polonica*). A secondary 'crenulation' of the ridges in some specimens is of possible comparable functional significance (offering increased attachment area/bonding) to that of the intricate pattern of micro-attachment points of the adductor muscle scars in some Recent cylindroleberidid myodocopids (see Kornicker 1975, fig. 265*c–e*).

In its biserial arrangement this distinctive muscle scar recalls that of platycopes such as cytherellids (see Van Morkhoven 1962, fig. 40) and, more pertinently, shares strong morphological similarities with Carboniferous entomoconchacean myodocopids (see Van Morkoven 1962, fig. 38; Kornicker and Sohn 1976, fig. 35) and particularly with Recent, oceanic thaumatocypridacean myodocopids (e.g. see *Thaumatoconcha caraionae* and *T. elongata* in Kornicker and Sohn 1976, figs. 35 and 44). In this context it is also taxonomically significant to note that Kornicker and Sohn (1976, p. 4, fig. 2) maintain that, based on cladistic analysis of the soft parts (eye; copulatory organ; appendages) of Recent myodocopids, entomoconchaceans and thaumatocypridaceans are not closely related to cypridinacean myodocopids.

'*Cypridinids*' (text-fig. 2E–H). One group of Silurian myodocopids have simple, oval, dome-like shells and differ considerably from bolbozoids in muscle scar pattern, in being relatively shorter and higher, and in lacking sulci or an anterodorsal bulb (see Pl. 84, fig. 1; Pl. 85, fig. 1; Pl. 87, figs. 1 and 2). The general designation 'cypridinid' is employed herein for these forms. Their shape and outline is comparable with Devonian and Carboniferous cypridinids (Bless 1973; Sohn 1977), Mesozoic myodocopids such as *Triadocypris* (Weitschat 1983), and particularly with the Recent cypridinacean families Cypridinidae, Philomedidae, and Cylindroleberididae (see Pl. 88; Kornicker 1975, 1981; Kornicker and Caraion 1978).
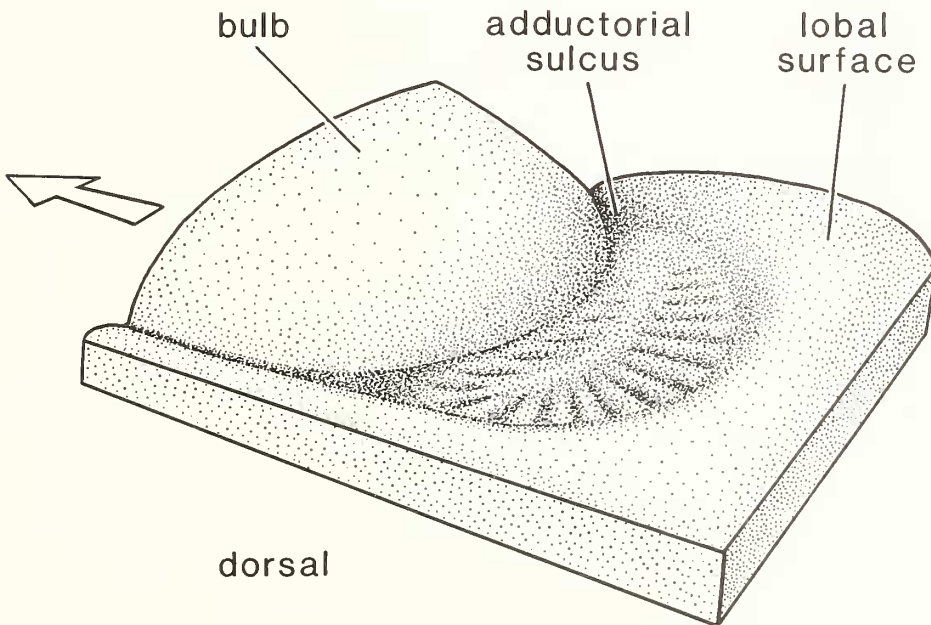
TEXT-FIG. 3. Schematic representation of adductor muscle scar of a Silurian bolbozoid ostracode (see Pl. 84, figs. 6 and 8); dorsal oblique view. Arrow indicates anterior.

TRUE ORNAMENT

Three types of external surface ornament have been recognized in Silurian myodocopids treated herein: reticulation, corrugation, and tuberculation (text-fig. 4). Similar ornament is also known in many fossil and Recent ostracode groups (see Sylvester-Bradley and Benson 1971 for details and terminology).

Reticulation (text-fig. 4A). Reticulation is frequently developed in bolbozoids, often occurring on all surfaces of the valve except for the upper part of the anterodorsal bulb, the rostrum, and the adductorial and posterior sulci (e.g. Pl. 84, fig. 7; text-fig. 5E, F). The reticulation consists of coarsely elliptical, ovoid, polygonal or, more rarely reniform fossae, each 200–600 μm across in adults. The deepest and widest fossae are normally in the ventral part of the valve (Pl. 84, fig. 7); medially, fossae often have an elliptical, elongate, or even sigmoidal shape (Pl. 84, figs. 4 and 7). The reticulum of young instars appears relatively less strongly developed and in some mature instars affects the whole shell thickness and is hence reflected on the internal mould. Reticulation also occurs in some Silurian 'cypridinids'; in 'Cypridinid' gen. et sp. nov. A a regular pattern of shallow, elliptical to polygonal fossae (each 100–300 μm across) covers the posterior half of the valve (Pl. 84, figs. 1 and 3).

Similar external reticulation is known from Ordovician to Recent in a wide variety of ostracode groups such as binodicopes (see Schallreuter 1980, 1983), palaeocopes (see Schallreuter 1982a, b), podocopes (see Benson 1971, 1973), and Recent myodocopids. The cypridinid *Scleroconcha flexilis* (Brady, 1898) and the philomenid *Anarthron chilensis* (Hartmann, 1965) are just two Recent myodocopids (Kornicker 1975, figs. 196 and 224) which illustrate similar reticulation to those of Silurian bolbozoids such as '*Bolbozoe*' cf. *bohemica* Barrande, 1872 (Pl. 84, fig. 7; Pl. 87, fig. 6).

As observed in podocopids, the pattern and form of external (polygonal) reticulation in ostracodes is closely determined by the arrangement of the underlying layer of individual epidermal cells (Okada 1981, 1982). The 'individual cell: polygon' correlation and the process of cell division were clearly demonstrated using growth series of Recent and fossil ostracodes. From the size and ontogenetic changes of their fossae, it is possible that the development of the reticulum was similarly controlled in Silurian myodocopids.

Corrugation (text-fig. 4B). A series of sigmoidal to sinuous and occasionally bifurcated grooves and ridges occurs in Silurian bolbozoids (e.g. Pl. 83, figs. 2, 4, 6) and 'cypridinids' (unpublished material from Morocco). Corrugation typically occurs throughout the lateral surface except on the sulci, rostrum, and upper part of the bulb (e.g. Pl. 83, figs. 2, 4, 6). Sometimes it seems best developed posteriorly and ventrally (e.g. Pl. 84, figs. 2 and 4). Juvenile bolbozoids have a relatively incomplete pattern of corrugation; ridges are shorter and less densely packed.
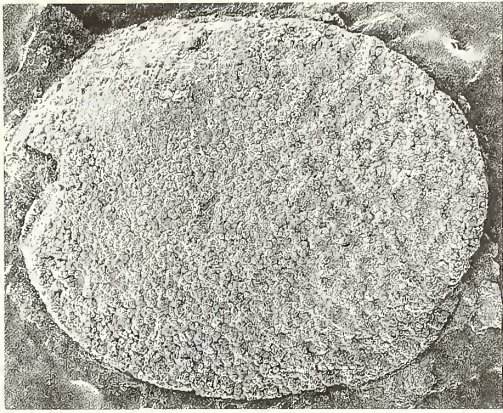

EXPLANATION OF PLATE 84

Examples of true ornament and adductor muscle scar patterns in Silurian myodocopid ostracodes.

Figs. 1, 3, 5. 'Cypridinid' gen. et sp. nov. A. Left valve IGR 33035, La Lande-Murée Formation, Les Buhardières (Andouillé, Mayenne), Armorican Massif, France. 1, lateral view, × 51. 3, detail of posterior surface reticulation, × 105. 5, reniform adductor muscle scar (and pattern of shell microstructures), × 225.

Figs. 2 and 4. '*Bolbozoe*' sp. nov. A. Right valve BM OS 13060. Long Mountain Siltstone Formation, Ludlow Series, Cause Castle Farm, Long Mountain, Powys, Wales. 2, lateral view, × 18. 4, detail of ventral part of the valve showing a combination of tubercles, corrugation, and reticulation, × 45.

Figs. 6–8. '*B.*' cf. *bohemica* Barrande, 1872. 6 and 8, right valve, IGR 33067, La Lande-Murée Formation, La Cultais (Vieux-Vy-sur-Couesnon, Ille-et-Vilaine), Armorican Massif, France. 6, lateral view, × 27. 8, radiate adductor muscle scar, dorsal oblique view, × 105. 7, lateral view of open carapace, IGR 33057, La Lande-Murée Formation, La Cultais (Vieux-Vy-sur-Couesnon, Ille-et-Vilaine), Armorican Massif, France, × 27.

All specimens are silicone rubber casts from external moulds. All SEM except fig. 7. BM = British Museum (Natural History), London.
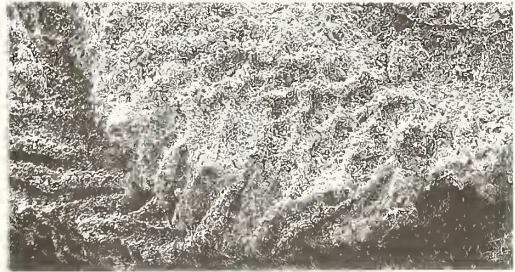
PLATE 84

SIVETER, VANNIER and PALMER, Silurian myodocopid ostracodes

tubercle   fossa

murum

A

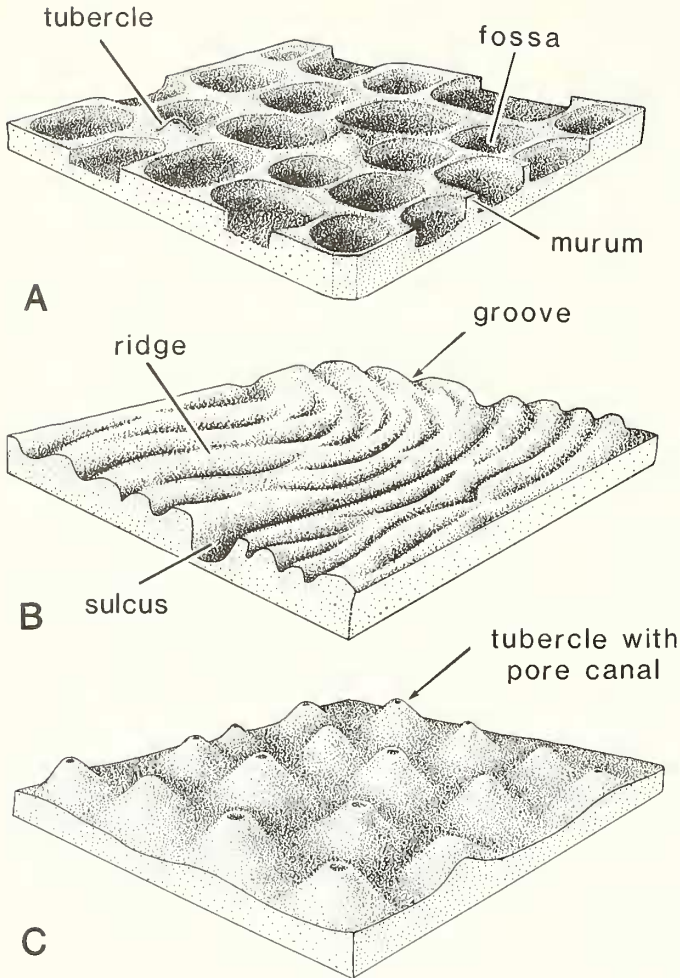ridge   groove


B sulcus

tubercle with
pore canal

C

TEXT-FIG. 4. Schematic representation of individual types of true ornament in Silurian myodocopid ostracodes. A, reticulation; B, corrugation; C, tuberculation.

In 'Bolbozoe' sp. nov. A most corrugations appear to run parallel to the sulci but ventrally they are aligned parallel to the ventral margin (Pl. 83, fig. 2). This pattern is strikingly comparable to that of the fossae in the dominantly reticulate bolbozoid 'B.' cf. bohemica (cf. Pl. 84, figs. 2 and 7) and also mirrors the alignment of tubercles in other Silurian tuberculate bolbozoids (e.g. Pl. 83, fig. 1). Seemingly the distribution of fossae, corrugations, and possibly tuberculation represent homologous patterns within groups of Silurian bolbozoids (text-fig. 5).

Forms of corrugation are also known, for example, in Palaeozoic platycopes (e.g. Schallreuter 1978), Mesozoic and Tertiary podocopes (e.g. Clements 1974; Doruk 1974), Recent polycope myodocopids (e.g. Hasan 1983), and Carboniferous entomozoids s.s. (e.g. Gooday 1983). Though entomozoids were traditionally classified as myodocopine myodocopids (e.g. Sylvester-Bradley in Moore 1961), as restricted to the 'fingerprint' ostracodes of current usage this group of Silurian–Carboniferous ostracodes lack characteristic features (e.g. rostrum and rostral incisure) of typical myodocopines and therefore belong outside that group. The arrangement and spacing of longitudinal and bifurcated primary ribs of several entomozoid taxa (e.g. see ?Kuzminaella sp. of Gooday 1983, fig. 10) are like the corrugated surface of Silurian bolbozoids. Gooday (1983) noted that shell ornament may not be reflected on the internal surface in entomozoids from the Carboniferous, a characteristic
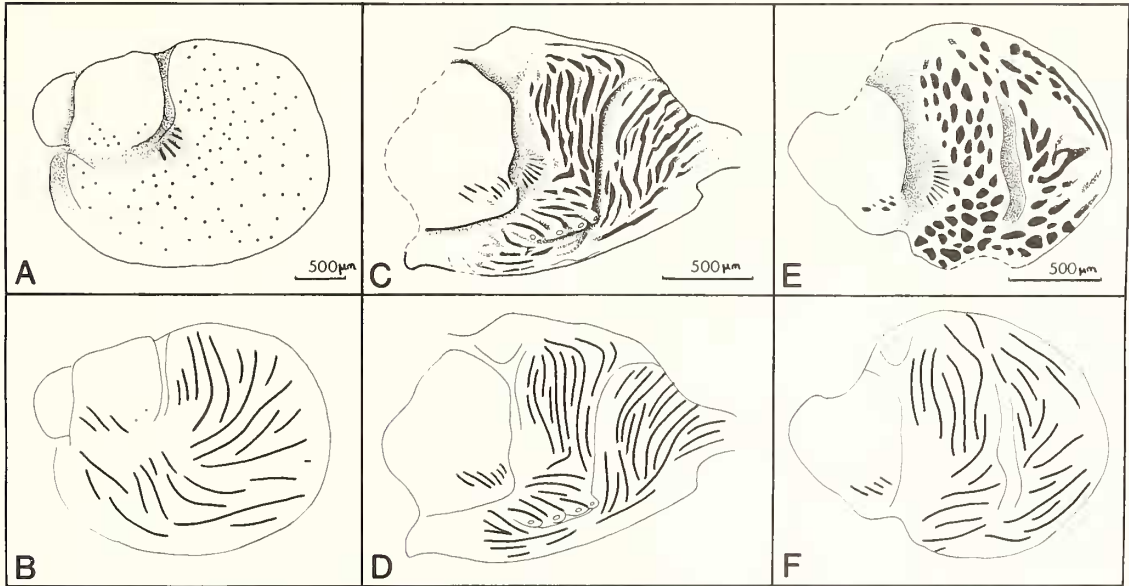
TEXT-FIG. 5. Valves (A, C, E) illustrating similar patterns of alignment (B, D, F) of tuberculation (A, B), corrugation (C, D), and reticulation (E, F) in bolbozoids. A, B, Bolbozoid gen. et sp. nov. A, based on right valve, IGR 33040 (valve reversed). C, D, '*Bolbozoe*' sp. nov. A, based on left valve, IGR 33048. E, F, '*B.*' cf. *bohemica*, based on left valve, IGR 33057.

also observed in many Silurian myodocopids. Ribbing may be an adaptation in entomozoids to a pelagic lifestyle (Gooday 1983; Siveter 1984) and it is possible, but again speculative, that the same may be the case for corrugations.

Tuberculation (text-fig. 4C). Tubercles are common in Silurian bolbozoids, though their number, size, and arrangement vary between taxa (cf. text-fig. 5A, C). In Bolbozoid gen. et sp. nov. A tubercles of *c.* 70–300 μm diameter cover lobes but not the sulci, rostrum, or dorsal part of the bulb (Pl. 83, figs. 1, 3, 5; text-fig. 5A). Most are regularly spaced, have a pore-like central perforation (Pl. 83, fig. 3) and show linear alignment (text-fig. 5A, B). Other bolbozoids such as '*B.*' sp. nov. A (Pl. 83, figs. 2 and 6; text-fig. 5C, D; Pl. 84, figs. 2 and 4) have only a ventral row of three to four tubercles in adults. In '*B.*' *bohemica* tubercles are more numerous and prominent in early instars, but are virtually lacking in adults. Tubercles can have expression on both internal and external shell surfaces in Silurian bolbozoids; the central perforation probably penetrates the shell thickness and may represent a normal pore canal communicating in life with the epidermal cells. Tuberculation is common throughout the Ostracoda as shown, for example, in palaeocopes (Martinsson 1962; Siveter 1976; Schallreuter 1982c), podocopes (Sylvester-Bradley and Benson 1971), and Recent myodocopids (Kornicker 1981, pl. 70).

Composite ornament (text-fig. 6C, D). Some Silurian myodocopids exhibit an intricate combination of reticulation, corrugation, and tuberculation (e.g. Pl. 84, figs. 2 and 4; text-fig. 6C, D). In '*B.*' sp. nov. A the reticulum centroventrally is surmounted by tubercles with pores and laterally merges with corrugations. This 'composite' external ornament has counterparts in Recent myodocopids such as *S. frons* (text-fig. 6A, B).

Normal pores. Though not ornament as such, the presence of normal pores in Silurian myodocopids is worth recording. Apart from having pores within tubercles, in one well-preserved specimen of
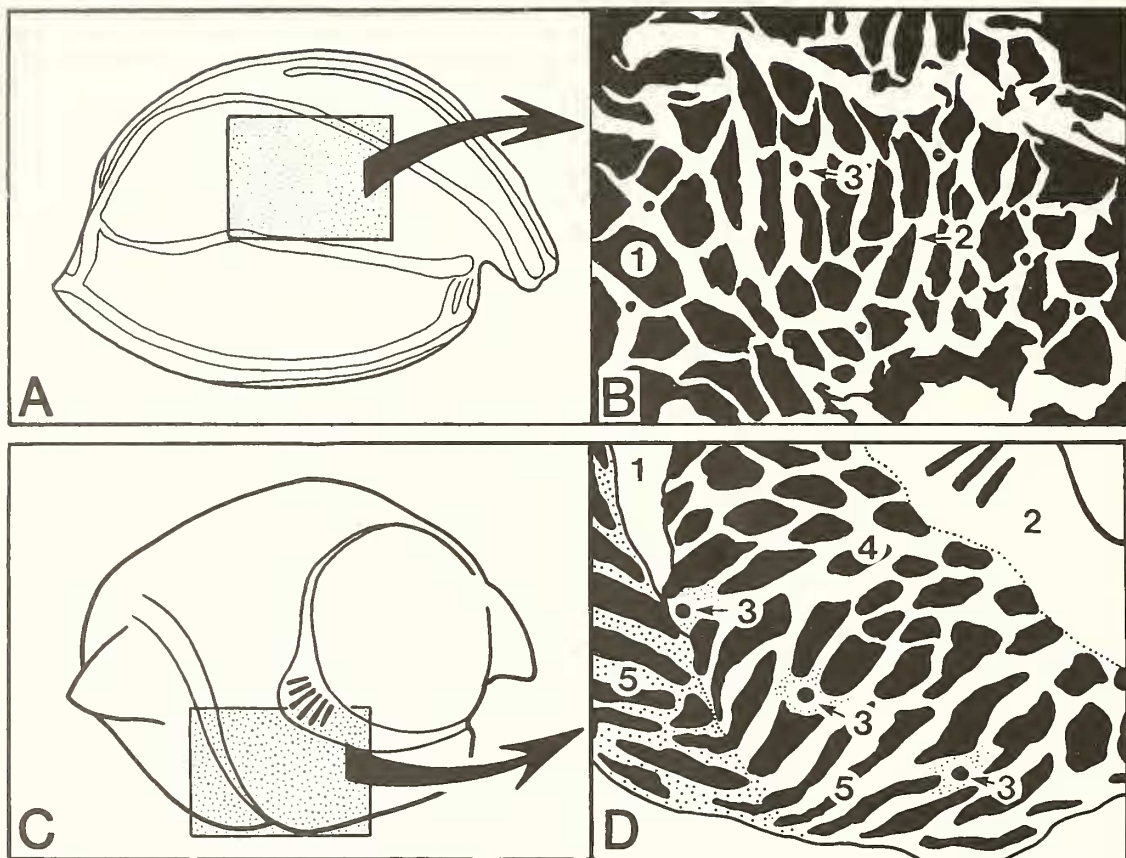
TEXT-FIG. 6. Comparison of true ornament in a Recent and a Silurian myodocopid ostracode. A, B, *Scleroconcha frons* Kornicker, 1975, philomedid, right valve (redrawn from Kornicker 1975, fig. 209a–b). Recent, SW Pacific off Chile; 1190–1263 m depth. A, lateral view, × 50. B, detail of the external surface ornament (reticulation), × 200. B1, fossa; B2, elongate fossa; B3, normal pore canal. C, D, '*Bolbozoe*' sp. nov. A, bolbozoid, right valve. Based on BM OS 13060 (see Pl. 84, figs. 2 and 4), Ludlow Series, Silurian, Long Mountain, Powys, Wales. C, lateral view, × 20. D, detail of external surface ornament, × 75. D1, posterior sulcus; D2, adductorial sulcus and muscle scar; D3, tubercles with pores; D4, reticulation; D5, corrugation.

Bolbozoid gen. et sp. nov. A (Pl. 83, figs. 1, 3, 5, 7, 8), pore-like structures were also observed anteroventrally. They consist of several single, circular and also double, semicircular openings about 30 μm in diameter, often with a central 'boss'. Comparable 'normal pores' occur in many Recent myodocopids: *Polycope choane* has sparsely distributed single and double pores on its lateral surface (Hasan 1983) and there are living cylindroleberidids with various types of minute, sparse, rimmed pores, pore groups, or tubed pores whose number and position can vary within a species (see Kornicker 1975, pls. 310, 320, 321).

In summary, the external sculptures of Silurian myodocopids described above are considered to be true, genetically controlled ornament, similar to that of many Recent myodocopids. Such features develop gradually and to a consistent pattern throughout the ontogeny of both Silurian and Recent myodocopid species. Lastly, patterns of reticulation, corrugation, and tuberculation in groups of Silurian myodocopids seem to be homologous (text-fig. 5) and the result of evolutionary processes rather than the chance factors.

SHELL MICROSTRUCTURES

Silurian myodocopids from the Welsh Basin, Armorican Massif, and Bohemia exhibit enigmatic, surface polygonal and radiate microstructures, each usually with a central perforation (Pls. 85–87).

Radiate microstructures. Subcircular radiate microstructures, herein termed rosettes (e.g. Pl. 85, fig. 3, *B.* cf. *anomala*), occur on both internal and external moulds, either individually; as clusters (e.g. Pl. 85, figs. 1, 2, 4, 5, 'Cypridinid' sp.; Pl. 87, figs. 6 and 7, '*B.*' cf. *bohemica*); more rarely as rosettes covering virtually the entire surface of the valve (e.g. Pl. 85, figs. 9–11, *B.* cf. *anomala*); and sometimes as tiny rosettes within a basically polygonal pattern of shell microstructure (see 'composite microstructure' below). Each rosette consists of some ten to thirty acicular radii and (excluding rosettes in composite patterns) is *c.* 100–500 μm across; most have a central perforation.

Polygonal microstructures. On the surfaces of both internal and external moulds of many of our Silurian myodocopids a pattern of relatively small, polygonal microstructures is discernible (e.g. Pls. 86, 87). The polygons vary in size (10–150 μm), shape (degree of elongation), outline (angular to more rounded), and packing (dense to loose) to give different types of patterns on the surfaces of the valves of several taxa. In three dimensions these structures are interpreted as polygonal platelets (text-fig. 9).

Typical polygonal patterns are shown in text-fig. 7. A specimen of *B.* cf. *anomala* (text-fig. 7A; Pl. 86, figs. 2 and 4) shows closely packed, centrally perforated polygons over almost all the external surface except the anterodorsal bulb; they are mostly irregular in shape, size (60–150 μm), and in the diameter of their central perforation. Similar polygons occur in a specimen of 'Cypridinid' gen. et sp. nov. B (Pl. 87, figs. 2–4). In another specimen of *B.* cf. *anomala* (Pl. 86, fig. 5, text-fig. 7B) the packing appears looser and some polygons ill-defined, though most have central perforations. Generally, the upper (outer) part of the central perforations of the polygons is often enlarged, such that each perforation can appear as a tiny concavity housing a minute hole (e.g. Pl. 86, fig. 4; Pl. 87, fig. 4; text-fig. 9).

Another common pattern consists of closely packed but smaller, rounded to polygonal, granule-like microstructures (each *c.* 10–60 μm diameter), some of which have a central perforation (Pl. 84, figs. 1, 3, 5; Pl. 87, figs. 1 and 5).

Composite microstructures. Radiate and polygonal microstructures of various sizes often occur in the same valve (text-fig. 9). For example, tiny radiate microstructures are often found intimately associated within a pattern of perforated polygons (e.g. Pl. 85, fig. 7, Bolbozoid gen. et sp. nov. A; Pl. 87, figs. 6 and 7, '*B.*' cf. *bohemica*). In many cases both the smaller, granule-like elements and the perforated polygonal platelets (combined range: 10–150 μm diameter) occur as a gradational,
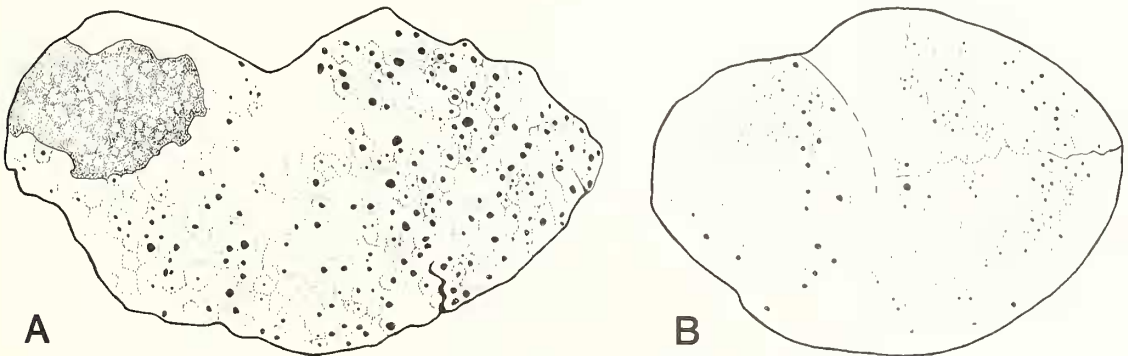
TEXT-FIG. 7. Pattern of perforated polygons on lateral surface of *Bolbozoe* cf. *anomala* Barrande, 1872. A, left valve, lateral view, IGR 33023 (see Pl. 86, fig. 2), × 25. B, left valve, lateral view, IGR 33029 (see Pl. 86, fig. 5), × 25.

intermingled pattern on individual valves (e.g. Pl. 87, fig. 4, 'Cypridinid' gen. et sp. nov. B; Pl. 87, fig. 5, 'Cypridinid' gen. et sp. nov. A).

The nature and origin of polygonal and radiate microstructures. The patterns of perforated polygons and radiate microstructures have many, shared characteristics which indicate that such microstructures should not be interpreted as true external ornament.

1. Their general distribution on valves appears to be random, with apparently no consistent trends in individuals or species.

2. In some specimens the microstructures are observed to be 'superimposed' on true ornament such as tubercles (Pl. 85, figs. 6 and 7), as well as on the adductorial sulcus (Pl. 87, figs. 6 and 7) and the rostrum (Pl. 84, fig. 1; Pl. 87, fig. 2), two regions where ornament is either otherwise unknown (adductorial sulcus of '*B*.' cf. *bohemica*) or not expected to occur (rostrum of Silurian myodocopids in general).

3. Critical evidence is found in some well-preserved carapaces which show a different polygonal pattern (Pl. 87, fig. 1) or arrangement of rosettes on the two valves. In one specimen a single radiate structure is developed only on the left valve (Pl. 85, fig. 3).

4. In contrast with the typical ornament of Silurian myodocopids (reticulation, corrugation) perforated polygons and radiate microstructures manifest complimentary patterns on both external and internal moulds.

5. Similar polygonal and radiate microstructures are found in various bolbozoid and 'cypridinid' myodocopid taxa from various localities of probably different ages. Compare, for example, the radiate structures in the specimen of 'Cypridinid' sp. from 'La Cultais' (Pl. 85, figs. 1, 2, 4, 5) with those of the specimen of *B.* cf. *anomala* from 'Les Buhardières' (Pl. 85, figs. 3 and 8); or compare the polygonal structures in the specimens of *B.* cf. *anomala* from 'Les Buhardières' (Pl. 86, figs. 1–6) with those of 'Cypridinid' gen. et sp. nov. B from Saint-Denis-d'Orques (Pl. 87, figs. 2–4).

Accepting this evidence that the shell microstructures are not ornament, they may have originated in one of several possible ways:

1. Microborings associated with endolithic fungi and algae occur in fragments of molluscs, echinoderms, coralline algae, barnacles, serpulids, and foraminiferans from shelf sediments (Perkins and Halsey 1971). Such activity produces different sizes (1–20 μm diameter), shapes, and patterns of perforations which are not dissimilar to those of some of the Silurian myodocopids. However, microborings in Recent material are never associated with complex, three-dimensional radiate or

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EXPLANATION OF PLATE 85

Examples of polygonal and radiate microstructures of the shell of Silurian myodocopid ostracodes.

Figs. 1, 2, 4, 5. 'Cypridinid' sp. Right valve, IGR 33054, La Lande-Murée Formation, La Cultais (Vieux-Vy-sur-Couesnon, Ille-et-Vilaine), Armorican Massif, France. 1, lateral view, × 75. 2, anterior oblique view, × 75. 4 and 5, details of acicular radiate structures ('rosettes') in anterior part of the valve (from 1 and 2 respectively; × 205, × 215).

Figs. 3 and 8. *Bolbozoe* cf. *anomala* Barrande, 1872. Open carapace, IGR 33025, La Lande-Murée Formation, Les Buhardières (Andouillé, Mayenne), Armorican Massif, France. 3, lateral view, × 56. 8, detail of perforated, acicular radiate structure ('rosette') on ventral part of the left valve, stereo-pair, × 380.

Figs. 6 and 7. Bolbozoid gen. et sp. nov. A. Right valve, IGR 33040, La Lande-Murée Formation, Les Buhardières (Andouillé, Mayenne), Armorican Massif, France. 6, lateral view, × 14. 7, detail of posteroventral part of external surface showing an acicular radiate structure ('rosette') on the side of a tubercle (*top right*) and closely packed perforated polygons (*lower left*), × 245.

Figs. 9–11. *B.* cf. *anomala* Barrande, 1872. Left valve, IGR 3300, La Lande-Murée Formation, Les Buhardières (Andouillé, Mayenne), Armorican Massif, France. 9, oblique ventral view, × 17. 10 and 11, details of closely packed radiate structures ('rosettes') on the lateral surface of the valve, × 200, × 150.

All specimens are silicone rubber casts from external moulds. All SEM except fig. 3.

PLATE 85
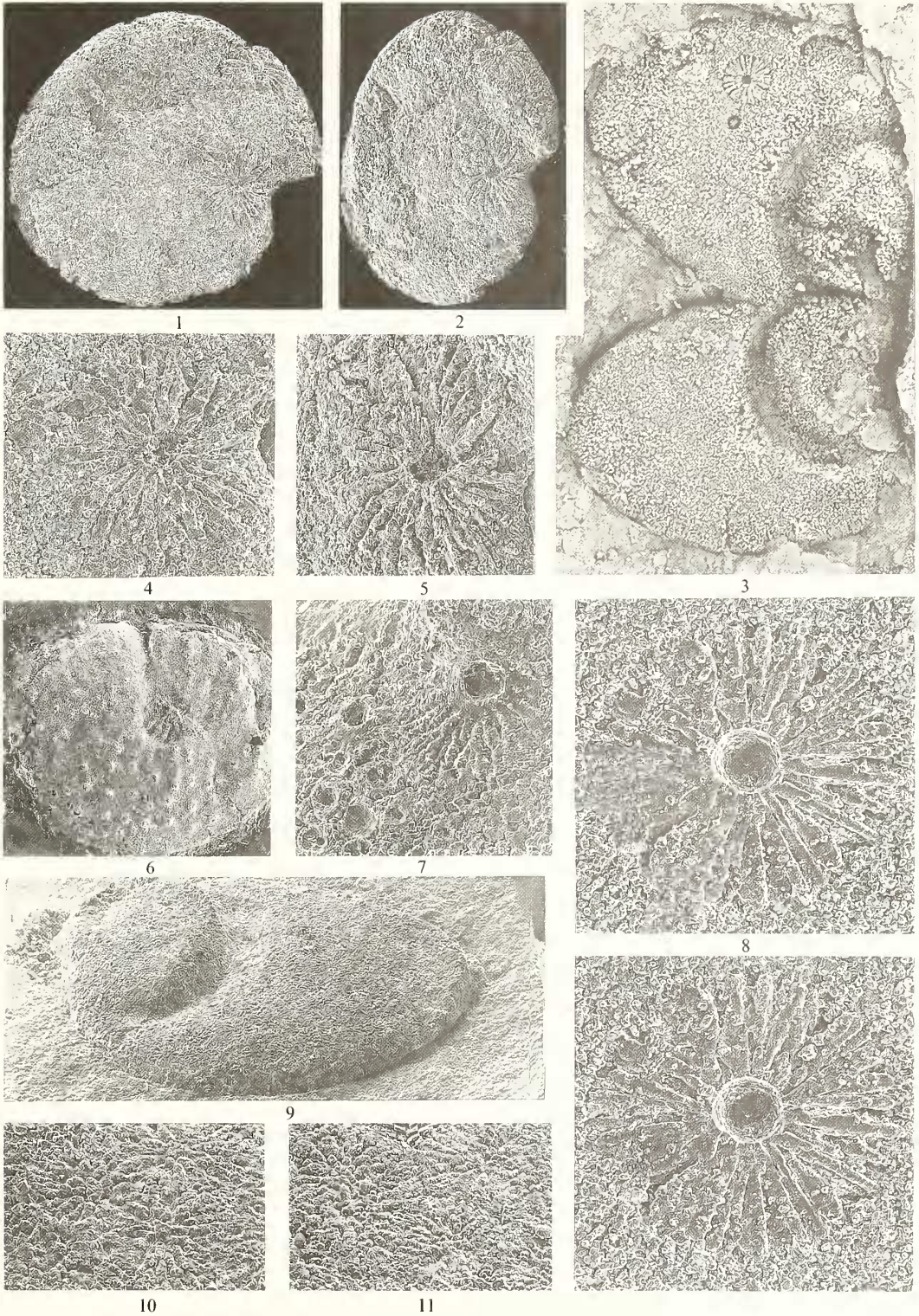
SIVETER, VANNIER and PALMER, Silurian myodocopid ostracodes
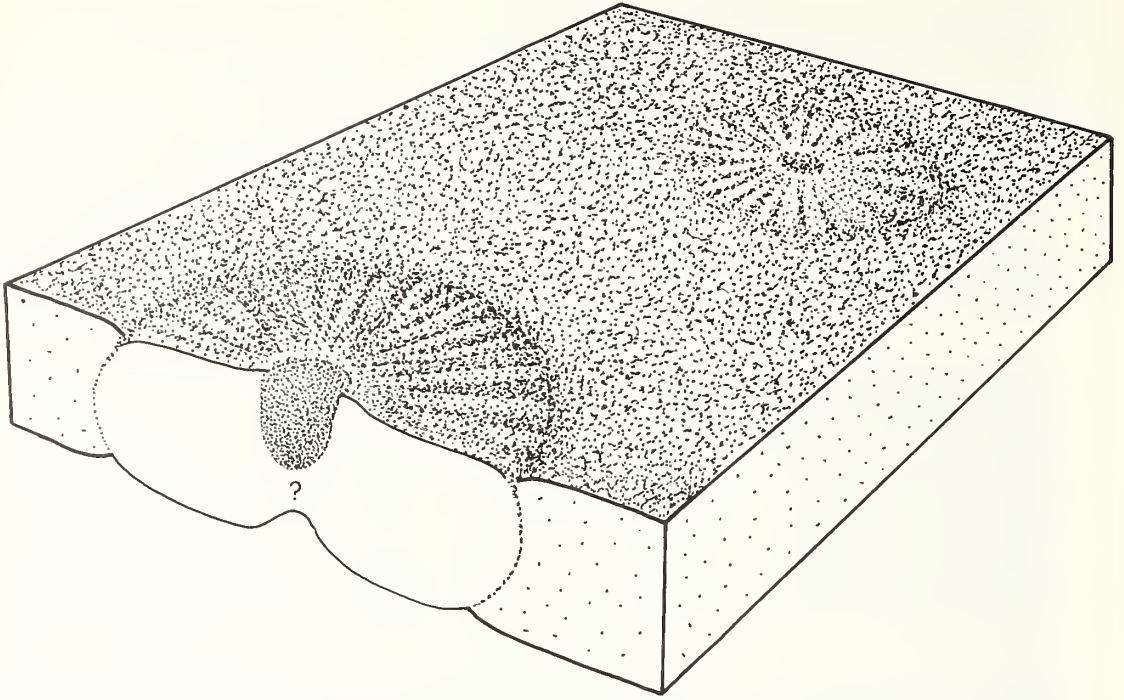
TEXT-FIG. 8. Reconstruction of acicular radiate structure ('rosette') based in part on observations on internal and external moulds of IGR 33025 (*Bolbozoe* cf. *anomala* Barrande, 1872; see Pl. 85, figs. 3 and 8). Central perforation may or may not completely penetrate shell thickness. True shell thickness unknown.

polygonal structures like those described from the Silurian myodocopids and such an origin is considered untenable.

2. It is possible that some kind of acidic action within the sediment might have produced these randomly distributed perforations and irregular polygonal patterns on the calcareous shells. Such acid erosion is unlikely for several reasons. First, the radiate structures and perforated polygons are lacking from associated faunas of palaeocope ostracodes, bivalves, eurypterids, and phyllocarids. Secondly, delicate external features such as muscle scars and minute pores are remarkably well preserved. Thirdly, the geochemistry of the Silurian black siltstones and mudstones indicates reducing conditions for the substrate (Dabard and Paris 1986).

EXPLANATION OF PLATE 86

Examples of polygonal and radiate microstructures of the shell of Silurian myodocopid ostracodes.

Figs. 1–6. *Bolbozoe* cf. *anomala* Barrande, 1872. 1 and 3, right valve, IGR 33027. 1, lateral view, × 22. 3, detail of packed, perforated polygons in ventral part of the anterodorsal bulb, stereo-pair, × 260. 2 and 4, left valve, IGR 33023. 2, lateral view, × 22. 4, detail of packed, perforated polygons in posterodorsal part of the valve, stereo-pair, × 260. 5, left valve, showing perforated polygons, IGR 33029, lateral view, × 22. 6, left valve, IGR 33026, lateral view, × 12, together with two other valves showing different types of external shell surfaces on the same slab (smooth surface; small, closely packed polygons; larger, packed, perforated polygons). All from La Lande-Murée Formation, Les Buhardières (Andouillé, Mayenne), Armorican Massif, France.

All specimens are Silicone rubber casts from external moulds. Figs. 1, 2, 5, 6 are light photographs; 3 and 4 are SEM.

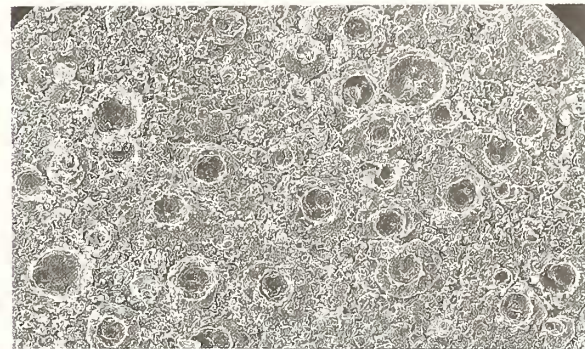PLATE 86

SIVETER, VANNIER and PALMER, Silurian myodocopid ostracodes
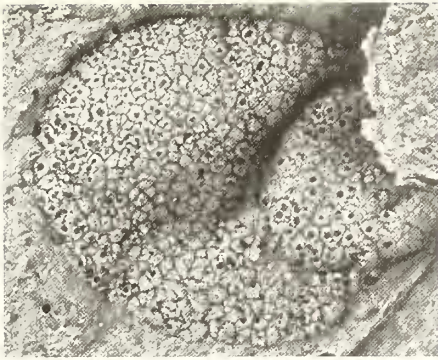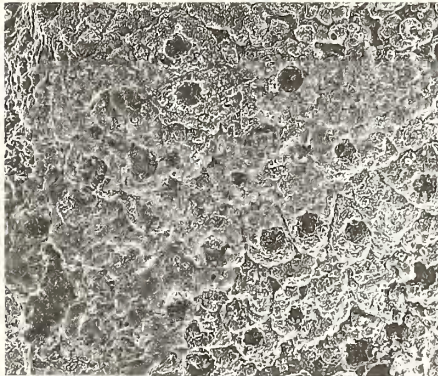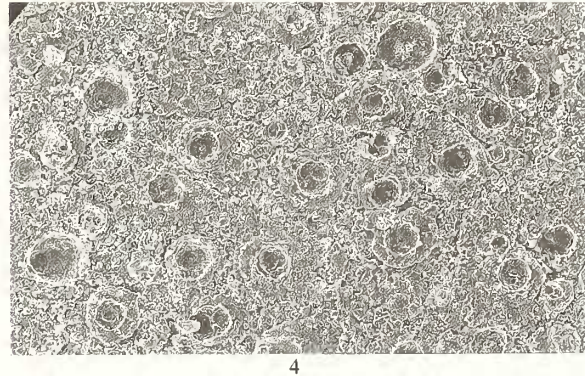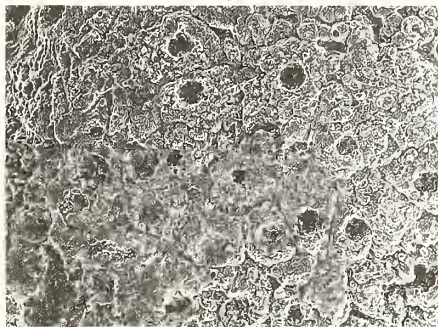
3. The origin of the radiate and polygonal microstructures may be directly related to processes concerned with shell calcification and its subsequent alteration. Radiate structures and perforated polygons are generally expressed on both internal and external moulds of individual valves, thus suggesting that the whole shell thickness is usually involved in the formation of these microstructures. Indeed, in one specimen (Pl. 86, fig. 5; text-fig. 7B) fracturing across the valve has clearly occurred in a zig-zag path, indicating boundaries between polygons. Three-dimensional reconstructions (text-figs. 8 and 9) depict individual radiate structures and perforated polygons each as internal and external surface expressions of isolated and coalesced platelets respectively. The central perforations may represent former normal pore canals although there is no firm evidence that they completely penetrate the thickness of the shell.

Bate and Sheppard (1982) have observed isolated and coalesced discs and spherulites of calcium carbonate within the cuticle matrix of Recent myodocopids, structures that they interpret as fundamental products of the *in vivo* calcification process responsible for producing the calcified ('shell') cuticle. According to these authors, growth of these structures appears to take place either by coalescence or by accretion around the disc ('plate') perimeter. The discs lie within and cut across the layers of chitin and observations under plane polarized light clearly show their radiate, crystalline nature (Bate and Sheppard 1982, pl. 2, figs. 1 and 2; herein Pl. 88, fig. 4). Such discs and spherulites, which are clearly present in the shell in many Recent myodocopids (see Pl. 88, figs. 1–8), share striking similarities with the platelets described herein from Silurian myodocopids: e.g. in size, shape (cf. Pl. 86, figs. 1–6 with Pl. 88, figs. 1–3), random distribution, coalescence (cf. Pl. 86, fig. 3 and Pl. 87, fig. 4 with Pl. 88, fig. 2), and the occurrence of central perforations (see Bate and Sheppard 1982). In addition, within their cuticle Recent myodocopids also show loosely packed (Pl. 88, fig. 1) and isolated platelets (Pl. 88, fig. 5). It is, therefore, possible that the radiate structures and perforated polygonal platelets in our Silurian myodocopids were produced by a similar process of shell calcification which may have taken place *in vivo*. Further, presumably post-mortem changes of the calcium carbonate platelets would then consist mainly of *in situ* recrystallization of the calcium carbonate, thus preserving most of their original form and arrangment. Under certain chemical conditions, the calcium carbonate of some platelets may have been rearranged to form acicular radiate structures (rosettes).

There is also, however, evidence based on several observations of Recent material, for an apparently entirely post-mortem crystallization of calcium carbonate matter in myodocopids. Discoidal, spheroidal, and irregular-shaped 'nodules' (up to 300 μm diameter) have been 'produced' within the cuticle of Recent cypridinid valves simply by drying the valves and then soaking them in water (Sohn

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EXPLANATION OF PLATE 87

Examples of polygonal and radiate microstructures of the shell of Silurian myodocopid ostracodes.

Figs. 1 and 5. 'Cypridinid' gen. et sp. nov. A. Open carapace, IGR 33016, La Lande-Murée Formation, Les Buhardières (Andouillé, Mayenne), Armorican Massif, France. 1, lateral view, × 15. 5, detail of central area of the left valve showing reniform muscle scar, perforated platelets and closely packed microplatelets, × 150.

Figs. 2–4. 'Cypridinid' gen. et sp. nov. B. Right valve, IGR 33200, siltstones of Ludlow or Pridoli age, Saint-Denis-d'Orques, Sarthe, Armorican Massif, France. 2, lateral view, × 18. 3, detail of adductor muscle scar (from 2), × 52. 4, packed, perforated polygons in anteroventral part of the valve, stereo-pair, × 52.

Figs. 6 and 7. 'Bolbozoe' cf. bohemica Barrande, 1872. Right valve, IGR 33059, La Lande-Murée Formation, La Cultais (Vieux-Vy-sur-Couesnon, Ille-et-Vilaine), Armorican Massif, France. 6, lateral view, × 9; note microstructures on dorsal part of the adductorial sulcus and on ornamented part of adjacent central lobal area. 7, detail of dorsal end of the adductorial sulcus showing radiate microstructures ('rosettes') and perforated polygons, stereo-pair, × 54.

Fig. 8. B. cf. anomala Barrande, 1872. Left valve, lacking any discernible microstructures, IGR 33018, La Lande-Murée Formation, Les Buhardières (Andouillé, Mayenne), Armorican Massif, France, × 19.

All specimens are Silicone rubber casts from external moulds. All SEM except fig. 6.

PLATE 87
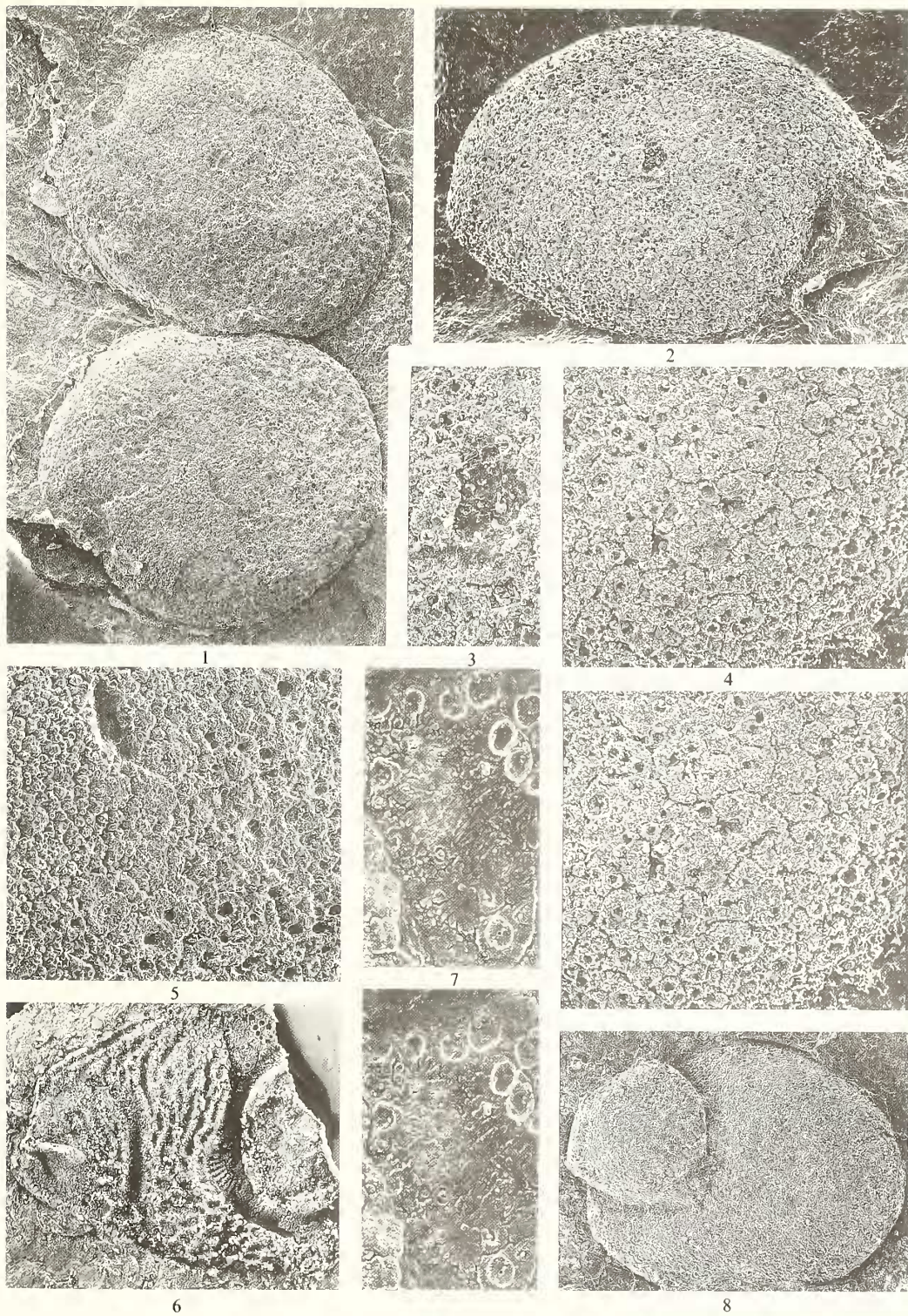
SIVETER, VANNIER and PALMER, Silurian myodocopid ostracodes
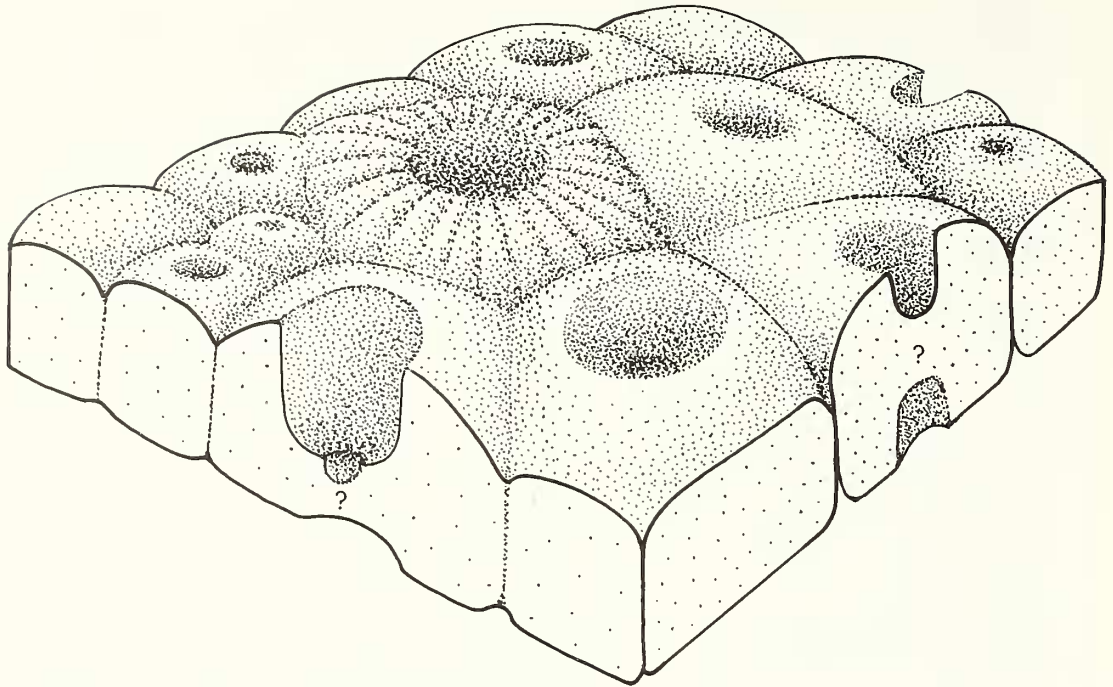
TEXT-FIG. 9. Reconstruction of packed polygonal platelets, including some showing acicular radiate structures; based on observations on internal and external moulds (e.g. see Pl. 85, figs. 6 and 7; Pl. 86, figs. 1–6). Central perforation may or may not completely penetrate shell thickness. True shell thickness unknown.

and Kornicker 1969). These nodules, of monohydrocalcite ($CaCO_3H_2O$) and calcite, are morphologically comparable to the platelets in our Silurian specimens and, according to the authors, can develop post-mortem in many Recent cypridinacean myodocopids. Sohn and Kornicker (1969, pl. 2, figs. 3 and 4) demonstrated that the initial form of the 'shell' carbonate in such valves is that of an amorphous gel evenly distributed throughout the cuticle; only subsequently is the carbonate redistributed during a change in form to monohydrocalcite, with nucleation leading to 'nodule' production. In addition, Kornicker (1981, herein Pl. 88, fig. 6) illustrated radiate, rosette-like structures produced by post-mortem mineral rearrangement within the cuticle matrix of a Recent myodocopid. Supposed post-mortem recrystallization (of possible platelets) occurs in Carboniferous cypridinacean myodocopids (see Sohn 1977; Bless 1973), where the obvious radiate markings consist of single or coalesced rosettes resembling those in Silurian myodocopids (cf. Pl. 85, figs. 9–11 with Sohn 1977, fig. 1h). Sohn (1977, p. 128) considered that the nodule 'artefacts' that Sohn and Kornicker (1969) induced in Recent *Vargula* specimens are not similar to the radiating structures seen in the Carboniferous '*Cypridina*' *radiata* and other species, but we are inclined to take the opposite view.

In summary, the evidence for the role and timing of the calcification process in Recent myodocopids is equivocal. Sohn and Kornicker (1969) emphasize the possibility of a very rapid posthumous production of crystalline nodules. They state, however, that the same process can also occur (though rarely) *in vivo*. Unfortunately they do not elaborate upon, or illustrate evidence for, this crucial statement. By comparison, Bate and Sheppard, in describing the process of cuticular spherulite (= nodule) development, appear to assume uncritically that it occurred *in vivo*, despite the fact that 'some non or poorly calcified individuals were present' (1982, p. 26). Furthermore, they seem to have been unaware of Sohn and Kornicker's earlier work and its fundamental implications for their own study. From this, and also because they do not record the preservational medium or give the

post-mortem age of their Recent specimens, it is difficult to assess the possible role that post-mortem processes may have played in the formation of the spherulites in Bate and Sheppard's material.

Ultimately this crucial question of the relative timing and role of the calcification process in the myodocopid cuticle can only be resolved by the study of living or freshly killed specimens. With regard to our fossil material we can say that it contains microstructures like those 'produced' in Recent myodocopid taxa and we therefore conclude that the same calcite depositional processes may well have been operative. Furthermore, the ubiquity of such structures in taxa separated in time by some 400 m.y. emphasizes that they cannot be of use in low level systematics.

There is, however, a further point that may lend weight to the argument for *in vivo* calcification in our fossil material. One of the main conclusions of Sohn and Kornicker's study was that their post-mortem interpretation for the calcification process explains 'the scarcity of fossil Myodocopida', since after 'the nodules formed, the protein and chitin framework of the shell usually disintegrated; consequently, recognisable myodocopid fossils are rare' (1969, pp. 104–105). However, our studies show that at least in certain Silurian environments, myodocopids can occur comparatively often and it could be that their relatively high preservational potential results from an early (*in vivo*) onset of the calcification process.

We suggest that a distinction can be drawn between various possible sequences of the implied calcification process and a model based on these differences is outlined below.

POSSIBLE MODE AND STYLES OF CALCIFICATION IN SILURIAN MYODOCOPIDS

The inferred presence of calcium carbonate platelets, comparable with those of Recent myodocopids (e.g. Bate and Sheppard 1982), within the shell of Silurian bolbozoids and 'cypridinids' implies a particular mode of calcification. However, the occurrence (within and between individuals of the same and different species) of a variety of sizes and styles of radiate and/or polygonal microstructures (Pls. 85–87) attributable to such processes clearly requires explanation. Taking into account the findings and *in vivo* interpretations of Bate and Sheppard (1982), a model to explain the possible mode of calcification and the formation of the various types of radiate and polygonal microstructures of the Silurian myodocopid shells is proposed (text-fig. 10).

Nucleation centres have obvious importance at the beginning of any calcification process. If such centres are numerous and densely packed, the resulting pattern of calcification will be very different than if they were sparse and distant. Thus, based on possible variation in number, density, and distribution of centres, four cases of shell calcification are considered in order to account for the formation of the variety of microstructures observed (text-fig. 10A–D). The central perforations present in most of the platelets of our Silurian myodocopids (text-figs. 7–9)—possibly normal pore-canals (see above)—provide in some cases possible nucleation centres. This has parallels in Recent myodocopids; Bate and Sheppard (1982) concluded that nucleation of calcium carbonate in *Halocypris inflata* might preferentially take place around pores.

Case A (text-fig. 10A, 1–4). Here the nucleation centres for initial calcification would be distributed regularly and densely across the cuticle matrix (Stage A1). Spherulites or discs of calcium carbonate begin to form heterochronously and grow outwards in all directions (Stage A2). Further calcification at new centres and peripheral accretion around existing discs produces a pattern of packed polygonal platelets which then effectively prevents further 'lateral' calcification taking place (Stage A3). At this stage the calcareous platelets are likely to be intimately associated with layers of chitin, as demonstrated by Bate and Sheppard (1982, pls. 5 and 6) in Recent myodocopids. As a result of possible microbiological action with the sediments the exuviae and post-mortem shells (Stage A4) would then probably lose any outer and internal organic (chitin) layers they might have had. At the same time and later some amounts of mineral recrystallization/rearrangement of the calcareous platelets would occur. Such a process would account for the formation of the granule-like, finely packed polygonal patterns (e.g. Pl. 84, fig. 5; Pl. 87, fig. 5).

Case B (text-fig. 10B, 1–4). Here, nucleation centres are less densely distributed and possibly correspond to normal pore canals (Stage B1). The calcification process is essentially similar to that in Case A, but with the possible growth of larger platelets. In Stage B4, a pattern of perforated polygons results, as seen after the degradation of organic matter (including the possible resultant enlargement of pore-canals) and a mineral rearrangement which included the development of a few acicular radiate microstructures (see Pl. 86, figs. 1–6; Pl. 87, figs. 2–4; text-fig. 9).

Case C (text-fig. 10C, 1–4). The number of nucleation centres (Stage C1) is sparser than in Case B. Post-mortem recrystallization produces a pattern of packed, perforated rosettes (Stage C4) (e.g. Pl. 85, figs. 9–11).

Case D (text-fig. 10D, 1–4). Here, centres of nucleation are very sparse and irregularly distributed (Stage D1). As in Cases A–C, spherulites grow outwards in all directions by peripheral accretion (stages D2, D3). The calcification process terminates before all the platelets could coalesce (Stage D3), because of the relatively large distance between nucleation centres. Post-mortem, acicular recrystallization then produces isolated rosettes (e.g. Pl. 85, figs. 3 and 8; text-fig. 8) or clusters of rosettes (e.g. Pl. 85, figs. 1, 2, 4, 5; Pl. 87, fig. 7).

Variation in the distribution and density of nucleation centres could explain the occurrence of various sized, closely packed platelets on the same valve (e.g. Pl. 87, figs. 3–5).

The model proposed (text-fig. 10) can be used to interpret cases where possible conspecific valves, often from the same horizon, locality, and (even) slab, show a variety of microstructures. For example, some specimens of *B.* cf. *anomala* are 'smooth' (Pl. 87, fig. 8), others show extensive patches of polygonal platelets (Pl. 86, fig. 5; text-fig. 7B), and yet others have a complete polygonal pattern developed (Pl. 86, figs. 2 and 4; text-fig. 7A). Most important and revealing as far as the interpretation of their various microstructures is concerned, are those conspecific valves occurring adjacent to each other on a single slab (Pl. 86, fig. 6). In this case the 'smooth' valves might possibly represent newly moulted individuals (text-fig. 10, stages A1, B1, C1, D1) with very small amounts of cuticle
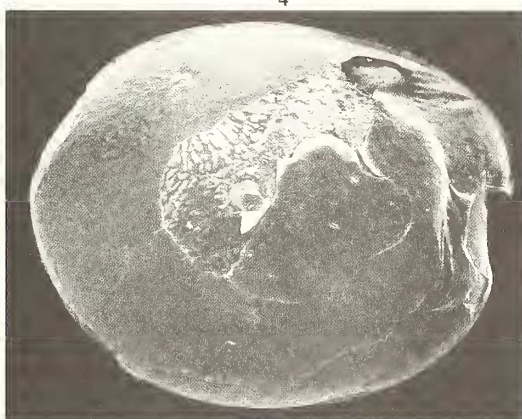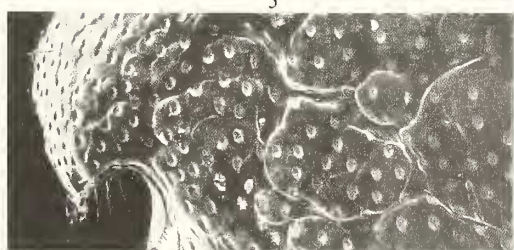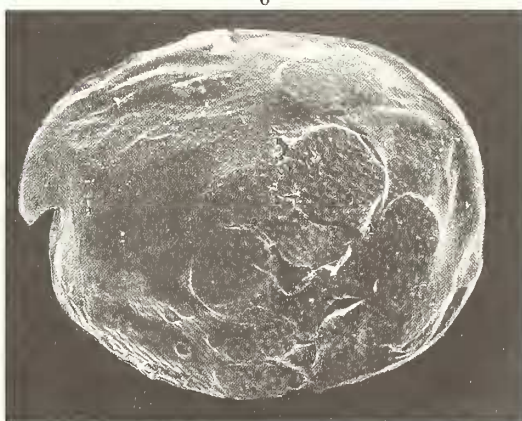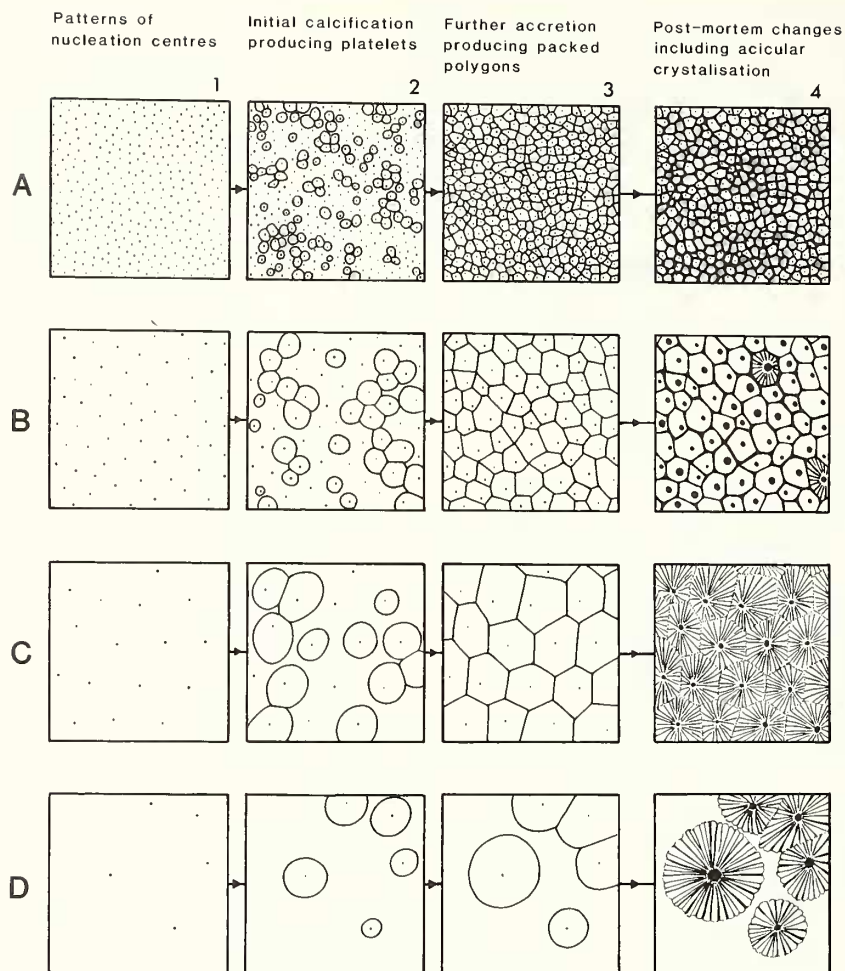

PLATE 88

SIVETER, VANNIER and PALMER, Recent myodocopid ostracodes

TEXT-FIG. 10. Model to explain the possible mode of calcification and formation of patterns of shell microstructures in Silurian myodocopid ostracodes. A, regular, densely distributed nucleation centres. B, C, less dense. D, irregular, sparsely distributed nucleation centres.

calcification (for detailed observations on the development of newly formed cuticle in ostracodes, see Rosenfeld 1979; Okada 1982). In the same way, patches of platelets on the valve surface might indicate an intermediate stage of calcification (text-fig. 10, stages A2, B2, C2, D2) or poor calcification, and specimens with relatively closely packed polygonal patterns have possibly completed their cuticle calcification prior to moulting anew (text-fig. 10, stages A3, B3, C3, D3). Such an interpretation is supported by observations (Bate and Sheppard 1982) on sympatric specimens of the Recent myodocopid *H. inflata*: some were fully calcified (having coalesced platelets forming a completely rigid shell), and others were either poorly calcified (patches of platelets) or lacked calcification (no platelets). Although not explicitly stated by Bate and Sheppard, these variations could reflect different states of calcification between moults. Another example, and particularly convincing in this context is the poorly calcified, 'in-moult' specimen of the Recent myodocopid *Tetraleberis maddocksae* figured by Kornicker (1981, pl. 34, fig. *a*; herein Pl. 88, fig. 5).

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